Inter-relating characters in the evolution of jumping spider (Araneae, Salticidae) behaviour, with special reference to *Trite planiceps* Simon

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ABSTRACT

Jumping spiders (Salticidae) differ from other spiders by having exceptionally acute vision and relying primarily on visual cues to mediate their behaviour. The unusual vision-dependent behaviours of salticids have become popular subjects of research based on 'the functional approach', a research paradigm that tends to treat each character as independent and emphasises natural selection as a mechanism explaining evolution. Using *Trite planiceps*, a New Zealand salticid, as a case study, this thesis examines how additional appreciation of the ways in which behaviour evolves may be gained when treating characters as inter-related and considering alternatives to natural selection. A series of specific examples investigating different types of inter-relationships between apparently unrelated behavioural characters of *T. planiceps* are presented and discussed. These examples consider (1) how change or stasis in one character may influence evolution of other characters (2) how a behaviour may incur costs in apparently unrelated contexts and (3) how trade-offs between different sources of fitness may influence the decision rules underlying flexible behaviours.

Much of *T. planiceps'* behaviour appears to be moulded around its unusual microhabitat of rolled-up flax leaves. This species' nest structure, intraspecific communication, and ability to attack and catch intruders in the absence of visual cues are all shown to be unusual in ways that suggest adaptation for this habitat. Apparently, habitat selection has had 'run-on' effects on each of these activities. On the other hand, current stasis in microhabitat preference likely constrains the evolution of each character to its current state. Like other salticids, *T. planiceps* females guard their broods, protecting them from predators. This character is conservative family-wide, and likely constrains the evolution of other salticid characters to pathways that do not compromise this vital activity.

Trite planiceps faces trade-offs between the anti-predator benefits of appendotomizing

(discarding) Legs I and costs of diminished ability during the seemingly unrelated contexts of intrasexual contests, courtship and hunting. An increased tendency to appendotomize legs might increase chances of surviving encounters with enemies, but selection for such an increased tendency is likely held in check by these opposing costs.

Trite planiceps is shown to have behavioural flexibility in contexts not previously reported for any salticid. *Trite planiceps* females make hunger-dependent decisions about whether to eat or guard their eggs and whether to ignore or associate with draglines of male conspecifics. They also make habitat-dependent decisions about whether to oviposit or delay oviposition. By matching behaviour with context, *T. planiceps* is able to expose behaviours to selection only when they are appropriate. Various currencies of success appear to be traded off against one another when choosing the most appropriate behaviour. For example, eggs are valuable both as progeny and as food, and which utility wins out will depend on the relative merit of the two.

In summary, I review the examples outlined in the various chapters throughout this thesis and place each in the context of what is known about salticid behaviour generally. I then question whether the functional approach has been applied appropriately in studies of salticid behaviour and whether additional insights might be gained by adopting a more holistic paradigm.

CHAPTER 1

General Introduction

"The conceptual framework of a scientific discipline determines to a large extent the direction of its progress and its ability to integrate the findings of related branches of knowledge into a meaningful body of facts and theories"

- Kaufmann (1961) in Ebert (1965)

From religion to research paradigms

Knowledge and understanding gained in any discipline is regulated largely by the kinds of questions that are asked. The transition brought about by popular acceptance of Darwin's ideas on natural selection is a poignant and instructive example of how underlying paradigms influence the kinds of questions, and answers, posed in queries of the world around us. Previously, God had been popularly considered sufficient explanation for all observed characters in all living things and the apparent perfection of living animals was deemed vindication that their origin must lie in the hands of a divine creator. Many clergymen were also naturalists, describing and cataloguing all the plants and insects around them, documenting the wonders of God's labour (systematists now document these same wonders of *evolution*; same job, different assumptions, different answers). The human world's view of itself was forever changed by the new paradigm placing *Homo sapiens* amongst the rest of the animal Kingdom as the product of "...nature red in tooth and claw" (Darwin 1859). But even Wallace, co-discover of 'natural selection', never seemed able to completely step out of the shadow cast through his life by

religious duty to the out-moded way of thinking that he had helped Darwin crucify.

Surprisingly, and contrary to popular belief, the 'scientific' approach to understanding speciation and the fit between animals and their environments favoured since Darwin and Wallace is far from devoid of subjectivity. Each scientist and discipline carries a characteristic perspective that influences the kinds of questions posed and therefore the kinds of answers gained in each field. Disagreements of scientific perspective between individuals and disciplines have led to controversy and vitriol to rival that between clergy and Darwinists. We must then ask whether our perception of the world around us is biased by subjectivity in the questioning process. Some of the most controversial subjectivities carry the names 'Functionalism', 'Structuralism', Holism', and 'Reductionism' (Sober 1984). Each of these terms refers to a particular "way of seeing" the universe (Hughes & Lambert 1984) that promotes very particular biases in the interpretation of how organisms evolve.

Ethology, the study of animal behaviour, has been dominated by functionalism ('the functional approach'; Jamieson 1986), also called the 'adaptationist program' (Gould & Lewontin 1979; Mayr 1983). Functionalism emphasises the role of natural selection as a mechanism explaining the evolution of observed characters. Functionalists tend to also be reductionists, dividing ('reducing') animals into discrete 'characters', and then studying the functions of each character in turn as though it is more or less independent of other characters (Sober 1984; Wimsatt 1984).

'Structuralism' is one alternative approach based on examining animals as 'integrated wholes', emphasising relationships between characters, and down-playing the importance of natural selection (see Hughes & Lambert 1984; Nagel 1984). Structuralists tend to be holists, percieving animals as 'integrated wholes' rather than as an assemblage of independently evolved characters. Functionalism and structuralism are sometimes portrayed as opposing extreme

positions but, in reality, most scientists take some middle path and are not completely ignorant of the pitfalls and merits of their passage. Nonetheless, the middle path stretches wide, and individual scientists differ considerably in what they percieve as an appropriate balance between the costs and benefits of these opposing perspectives.

Criticisms of the functional approach

In recent years, there has been strong criticism of the functional approach as a research paradigm (e.g., Gould & Lewontin 1979; Jamieson 1986), especially in relation to ethology (e.g., Gray 1986, 1988). Critics have questioned what appears to them to be an *a priori* assumption that evolution of all identifiable behaviours is primarily an account of natural selection (e.g., Jamieson 1986). Functionalists have been accused of studying adaptation, rather than evolution *per se*, and the functional approach has been caricatured as 'pan-selectionist' (e.g., Gould & Lewontin 1979) or even as substituting natural selection for God as the creator (Hailman 1988). Gray (1988) accuses functionalists of paying lip-service to constraints on adaptation, rather than truly incorporating these constraints into their methods.

Many authors have also criticized the functional approach for being excessively reductionist (e.g., Gould & Lewontin 1979; Ho 1988). Bock (1991) aptly summarises the critics opposing view: "features do not exist as seperate entities, but are always found in complex systems possessing tight organization known as individual organisms which in turn do not exist as separate entities but always in relationship with their external environment." Critics claim that by reducing animals into sets of discrete characters, and then examining each of these characters in isolation, functionalists underestimate the importance of inter-relationships between characters.

Defending the functional approach

Some advocates of the functional approach have responded to the claims of their critics (e.g., Maynard Smith 1982; Thornhill & Alcock 1983; Krebs & McCleery 1984; Mitchell & Vallone 1990; Guilford & Dawkins 1992). In one of the most lucid accounts, Mayr (1983) accuses Gould & Lewontin (1979) of "breaking in open doors", and claims that their criticisms are directed toward an inaccurate portrayal of the functional approach. Specifically, Mayr (1983) suggests that Gould & Lewontin's (1979) portrayal of the functional approach as pan-selectionist is unwarranted. Correctly applied, the functional approach refers only to an emphasis on, not a strict and exclusive adherence to, hypotheses built around natural selection. Nevertheless, even Mayr (1983) concedes that functionalists should indeed pay greater attention to constraints on adaptation than some have in the past.

Claims of excessive reduction in the functional approach also require attention. That reduction may lead to an under-estimation of relationships between characters is acknowledged by Mayr (1983). However, reduction may be justified by practical considerations. Reduction allows researchers to restrict attention to only those characters that are considered to be of greatest importance, thereby allowing more manageable, tractable, questions than when many variables are considered (Sober 1984; Hailman 1988). Tractability is traded-off against artificiality; "The student of adaptation has to sail a perilous course between a pseudoexplanatory reductionist atomism and stultifying non-explanatory holism" (Mayr 1983). However, we can still ask whether the degree of reduction is too frequently excessive; there may be a need to encourage in functionalists a greater awareness of animals as integrated wholes.

Understanding the behaviour of jumping spiders

My interest in trying to understand the evolution of animals and their behaviour as integrated wholes has led to a more specific interest in the behaviour of jumping spiders (Salticidae). Salticids are unique amongst spiders in that they have complex eyes and acute vision (Blest 1985a; Land 1985). Accordingly, salticids make greater use of visual cues to mediate their behaviour than do spiders from other families. Instead of building webs, most salticids actively hunt their prey, relying on vision for navigation (Hill 1979; Forster 1982a; Tarsitano & Jackson 1992; Jackson & Wilcox 1993a) and to mediate hunting sequences (Drees 1952; Gardner 1964, 1966; Forster 1977a, 1979). Salticids also possess elaborate repertoires of visual displays for use during intraspecific interactions (Crane 1949; Jackson 1982a; Richman & Jackson 1992).

Unsurprisingly, studies of salticid behaviour have emphasised their unique, visually mediated, behaviours (e.g., Crane 1949; Drees 1952). Also, most of the published research of salticid behaviour has been based, more or less explicitly, on the functional approach (e.g., Jackson 1978a, 1980a,b; Jackson & Wilcox 1990, 1993b). However, the appropriateness of the functional approach as applied to the study of salticid behaviour has rarely been considered (but see Jackson 1992). In this thesis, I ask whether a more complete understanding of salticid behaviour might be gained by following a more holistic approach with greater emphasis on inter-relationships between characters and explicitly recognising the importance of evolutionary mechanisms other than natural selection. Specific examples of inter-relationships between different characters of *Trite planiceps* Simon (Salticidae) are presented as an instructive case study.

Trite planiceps: a case study

Certain aspects of the natural history of *Trite planiceps* Simon appear to make this species an especially suitable subject for a study of inter-relationships between different characters. This species is geographically widespread within New Zealand, but appears to have a close relationship with a special and unusual microhabitat; the cavities formed by rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants (Forster & Forster 1973; Forster 1979). Although *T. planiceps* has been used in various comparative studies of predation (e.g., Forster 1979; Jackson & Van Olphen 1991), navigation (Tarsitano & Jackson 1992) and pheromonal communication (e.g., Jackson 1987), there has been no previous investigation specifically studying the life history and behaviour of this species.

Evolutionary cascades and functional constraints

Recognising that characters are inter-related, it becomes important to consider how change in one character may influence the evolution of other characters. Gray (1988) discusses 'ecological and evolutionary cascades' whereby evolution may be viewed as 'autocatalytic', with change in one character leading to widespread changes by moving the animal into a new 'adaptive zone' (*sensu* Simpson 1953). A spider's habitat determines largely the selection pressures to which it is exposed through, for example, the types and abundance of prey, predators, and shelter encountered. Accordingly, changes in habitat may lead to widespread changes throughout a wide range of characters and habitat may be an important starting point for ecological and evolutionary cascades. *Trite planiceps*' habitat, the cavities formed by rolled-up leaves of New Zealand flax, may have exposed this species to habitat-specific problems that may have promoted the evolution of habitat-specific adaptations.

In the first 3 chapters of Section I, I consider the ways in which *T. planiceps*' habitat

may have influenced characters that, at first sight, are not obviously related to habitat. In particular, I consider the influence of habitat on nesting and signalling behaviour (Chapter 2) the cues used to find mates (Chapter 3), and how responses to intruders in the absence of visual cues may be modified by the frequency of similar encounters in nature (Chapter 4).

Just as ecological and evolutionary cascades may stem from a small change in one characters, stasis or evolutionary conservatism in one character may limit evolution in others. Oyama (1988), Dullemeijer (1991) and Williams (1992) emphasise that evolution is as much about what may not exist as it is about what does exist. Although their emphasis is on structural constraints, the current utility of one behaviour may also constrain evolution by determining which alternative evolutionary paths are adaptively viable ('functional constraints': Dullemeijer 1991). Consequently, evolutionarily labile characters may tend to 'evolve around' and compensate more static, conservative characters.

Maternal brood-attendance is an apparently conservative feature in salticids, being both widespread and phylogenetically ancient (see Richman & Jackson 1992). Following oviposition, female salticids usually remain with their brood until the juveniles disperse. What is it about brood-attendence that makes this character so conservative amongst salticids? Several authors (e.g., Eberhard 1974; Richman & Jackson 1992) have suggested that brood-attendence may be maintained by functioning as brood-defence and in Chapter 5 I investigate this possibility. Strong selection for brood-defence, the proposed function of brood-attendance, may constrain the evolution of other characters to pathways that do not compromise this important task.

Functional conflicts

A second important way in which different characters may interact is when disparate selection pressures simultaneously operate on a single character. When selection pressures are in conflict, increasing adaptedness in response to one selection pressure may compromise adaptedness in terms of opposing selection pressures. "Most traits constitute trade-offs between a negative effect on the individual's fitness (cost), often by decreased efficiency of other characteristics, and a specific positive effect (benefit)" (Hasson 1994).

Trite planiceps appears to face an interesting conflict between selection on the various functions performed by Legs I and the ability to appendotomize Legs I as a means of escaping predators. The benefits of increased chances of survival that are gained through appendotomy (see Eisner & Camazine 1984; Formanowicz 1990; Dodson & Beck 1993) may be countered by costs incurred by decreased ability to perform activities during which intact spiders use these legs. *Trite planiceps* uses Legs I for signalling during intrasexual contests and courtship, and to grasp prey (Forster 1977, 1982). In Section II, I investigate whether the anti-predator adaptation of appendotomizing Legs I imposes costs due to reduced fighting ability (Chapter 6), reduced ability of males to court females (Chapter 7), and reduced prey-catching ability (Chapter 8).

Behavioural flexibility

Selection pressures moulding the decision rules that underlie behavioural flexibility are a third important way in which characters may interact. Animals with behavioural flexibility possess several disparate behaviours and a set of decision rules that determine which behaviour is selected (see Jackson 1992). The decision rules are based on the relative appropriateness of each option under present conditions; the most appropriate behaviour is chosen and others are

concealed. Behavioural flexibility allows animals to temporarily hide inappropriate behaviours from selection. This allows behaviours that would usually be disadvantageous to evolve alongside usually advantageous and usually expressed behaviours without competing directly (see West-Eberhard 1989). Behavioural flexibility allows animals to minimise interference (conflicting selection pressures) between characters.

Examination of behavioural flexibility, especially conditional strategies, may also be a useful source of evidence validating emphasis on functional hypotheses in studies of salticid behaviour (see Jackson 1992). Behavioural flexibility represents simultaneous adaptedness for more than one temporally isolated condition. Because it is usually expected that adaptation occurs more rapidly or more completely in characters that are frequently exposed to selection, adaptedness in characters that are only occasionally exposed to selection or the ability to adaptively select options that are only occasionally useful, may highlight the pervasiveness of natural selection.

Salticids are well-known for behavioural flexibility in predation and communication (Jackson & Hallas 1986a; Jackson 1986c, 1992; Edwards & Jackson 1993). Some salticids use several different predatory tactics, and males of most salticids use different courtship and mating tactics, depending on the maturity and location of females. In Section III, I investigate two previously unstudied instances in which *T. planiceps* may use behavioural flexibility to match behaviour with circumstance. First, I investigate whether *T. planiceps* can delay oviposition when suitable nesting habitat is unavailable (Chapter 9). Such an ability would allow spiders to take account of the relationship between nesting site quality and associated risks to their offspring and the relationship between time and associated costs of delaying oviposition. I then investigate whether individual *T. planiceps* base decisions about whether to associate with conspecific's draglines on foraging considerations (Chapter 10). Some salticids are known to

use cues from draglines when seeking mates (Yoshida & Suzuki 1981; Clark & Jackson 1994). Perhaps salticids also use cues on draglines to seek conspecifics as prey when hunger renders such a dangerous quarry worthwhile.

In Chapter 11 I review and summarise the insights gained by emphasising inter-relationships between different characters in the evolution of behaviour in *T. planiceps* and other salticids. I also reconsider the wider question of whether the functional approach currently used to study salticid behaviour strikes an appropriate balance between costs and benefits of reductionism and takes adequate heed of evolutionary mechanisms other than natural selection.

SECTION I

Evolutionary cascades and functional constraints

CHAPTER 2

A role for habitat in the complex communication of *Trite planiceps* Simon (Araneae, Salticidae)

ABSTRACT

The natural history and intraspecific interactions of *Trite planiceps*, a common New Zealand jumping spider (Salticidae), are qualitatively described for the first time and discussed in relation to this salticid's unusual microhabitat; rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants. In many respects, *Trite planiceps'* display and mating behaviour resembles other salticids. Males have conditional courtship and mating tactics, and tactics used depend on the female's maturity and location. If in light, the male uses visual courtship and mates in the open; if at a nest (inside a rolled-up leaf), the male uses vibratory courtship and mates inside the rolled-up leaf; if the female is immature, the male cohabits until the female matures, and then mates inside the rolled-up leaf. Regardless of which courtship tactic is used, after males mount females there is a phase during which the pair are in physical contact and communicate using tactile signals ('post-mount courtship'). When in light, away from rolled-up leaves, other sex and age classes of *T. planiceps* also communicate using visual displays, and also sometimes employ tactile signals during escalated contests.

But in addition to these typical salticid characteristics, *T. planiceps'* display repertoire also includes some very unusual elements that appear especially appropriate, and likely adapted, for communicating in its unusual habitat. Even when no conspecific has been encountered, *T. planiceps* males sometimes display when approaching openings of rolled-up leaves that contain,

or have been recently occupied by, females. These displays closely resemble visual displays used while facing a conspecific male in light. Later, while entering cavities within rolled-up leaves and while moving about inside simulated rolled-up leaves (glass tubes kept away from visible light and observed using infra-red video), males and females appear to use vibratory signalling, tapping the leaf surface with Legs I and twitching their abdomens, even when no conspecific has been encountered. Finally, when spiders interact within these cavities, they appear to communicate using an array of tactile and vibratory signals, tapping each other and the substrate with Legs I and with palps, twitching their abdomens, and lunging forward while holding onto the substrate. *Trite planiceps* appears to propagate vibratory signals not only through nests, a medium often used by other salticids, but also through the leaves forming the cavity walls. This is the first study using infra-red video to observe salticid interactions that usually occur in darkness and is also the first report of a salticid possessing a display repertoire for use in darkness away from nests. The relationship between habitat and signalling behaviour of salticids generally is discussed.

INTRODUCTION

Jumping spiders (Salticidae) differ from other spiders by having complex eyes and exceptionally acute vision (Land 1985; Blest *et al.* 1990). In association with their unusual visual abilities, salticids have evolved extraordinary visual navigating and hunting abilities (Jackson & Wilcox 1993a; Jackson 1992) and include some of the most dramatic examples of visual communication amongst invertebrates (Forster 1982c; Clark & Uetz 1994). Many salticids are strikingly ornamented and rely on elaborate courtship and threat displays when interacting with conspecifics (Crane 1949; Forster 1982c; Faber & Baylis 1993). Although some spiders from other families do use visual displays (e.g., Lycosidae; Aspey 1976;

Fernandez-Montraveta & Ortega 1993), the displays of salticids are uniquely elaborate.

Early studies of salticid communication focused almost exclusively on visual signalling (Peckham & Peckham 1889, 1890; Heil 1936; Drees 1952). But more recent studies have revealed conditional signalling strategies that also include repertoires of vibratory signals for use when interacting with conspecifics out of view inside nests, and tactile signals for use when touching conspecifics (Jackson 1992). Salticids are remarkable not just for elaborate visual signalling, but also for extreme variety and flexibility of signalling in different senses.

Although salticids generally resemble one another by possessing visual signalling and conditional signalling strategies, closer scrutiny reveals considerable interspecific variation in signalling behaviour (Richman 1982; Jackson & Hallas 1986a). For example, salticids vary in complexity of conditional signalling strategies, with some species relying on visual signals even when at nests (Jackson & MacNab 1991). However, the reasons why salticids differ in signalling behaviour are poorly understood.

Physical qualities of interaction sites can influence signal design (Endler 1992), and may partly explain interspecific variation in salticid signalling. For example, salticids that use visual signals even when at nests tend to have open nest structures and would have greater opportunity to see one another during these interactions than do salticids with more enclosing nests (Jackson & MacNab 1991). Also, species that live on elastic substrates, such as leaves and webs, have greater opportunity for evolution of vibratory signalling than species living on inelastic substrates. In the present study, *Trite planiceps* has been selected as a useful illustration of how salticid display repertoires may be moulded by physical qualities of the sites where conspecifics meet.

Trite planiceps commonly inhabits the dark cavities formed by dessicating, rolled-up leaves of New Zealand flax (*Phormium tenax*; Fig. 1) and similar plants (Forster 1979). These

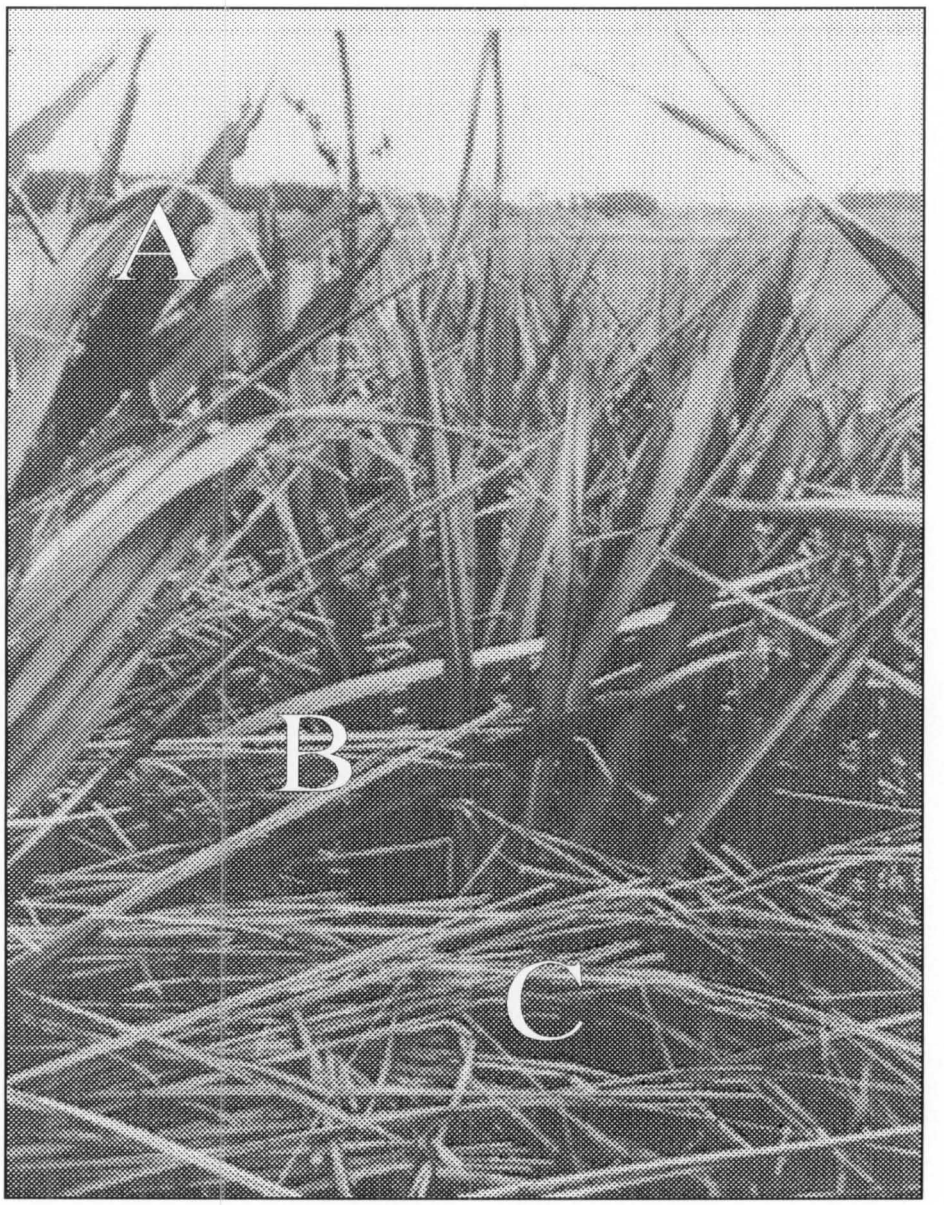

Figure 1. New Zealand flax plants (*Phormium tenax*), the typical habitat of *Trite planiceps* (taken at the sight from which spiders were collected for the present study). (A) green, open leaves. (B) dry, rolled-up leaves. (C) rotting, wet rolled-up leaves.

1-2 m-long leaves are usually oriented betwen 45° up from the ground and vertical, and the cavities within them are tube-like with a single opening, just large enough for a spider to pass. This is a very unusual habitat for a salticid, and *T. planiceps* would interact with conspecifics in sites with physical qualities that would not be experienced by other salticids; as well as encountering conspecifics in light and at nests (the typical salticid interaction sites), *T. planiceps* would also encounter conspecifics in darkness within the rolled-up leaves with no nest present to carry vibratory signals.

Because habitat-specific signalling behaviour might be overlooked when using the simple arenas traditionally used when studying salticid interactions (Jackson & Hallas 1986a), I stage interactions in arenas designed to simulate interaction sites in nature. This includes the unprecedented use of infra-red video to study salticid interactions that would normally take place in darkness. Forster (1982c) presents preliminary observations of contests between *T. planiceps* juveniles. Forster's findings suggest that this species' visual display repertoire is large and varied and that size is an important predictor both of contest outcome and of behaviour during contests. Studies of other salticids suggest that residency may also be important in salticid contests at nests (Jackson & Cooper 1991). Building on these earlier findings, I investigate how relative size, sex and residency status influence the interactions of *T. planiceps*.

MATERIALS AND METHODS

Collection and maintenance of spiders, and observations in nature

Spiders were collected from dense stands of New Zealand flax (*Phormium tenax*) near Christchurch, New Zealand. Standard procedures were used for maintenance and terminology, including the convention that the terms 'usually' or 'generally', 'sometimes' or 'occasionally', and 'infrequently' or 'rarely' indicate frequencies of 80% or more, 20-80%, and 20% or less,

respectively (Jackson & Hallas 1986a). 'Male' and 'female' refer only to adults, 'subadults' are spiders in their penultimate instar, and 'juvenile' includes all active stages prior to the penultimate instar. Observations in nature were mostly carried out while collecting spiders at various times over two years.

Procedures for observing interactions in the laboratory

For all interactions, pairs of spiders were randomly selected from a laboratory population, with the exceptions that no individual spider was used more than three times in any interaction type (e.g., male-male) or allowed to interact with a conspecific that it had encountered previously. Interactions were not staged within 2 h of the beginning or end of the laboratory light phase (12L:12D).

Although preliminary observations were staged in simple arenas using standard procedures (Jackson & Hallas 1986a), interactions described here were staged using arenas designed to simulate the sites where interactions would take place in nature. Use of arenas that simulate natural sites should permit a more realistic and complete impression of displays and interactions than might be achieved using simple, standard, arenas.

Encounters naturally occurring on leaves in daylight

Encounters that would naturally occur on leaves in daylight were staged on an arena designed to simulate the long, narrow leaves of the flax plants from which spiders were collected (Fig. 2). The arena comprised a platform of polyacetate (70 mm wide, 300 mm long) covered with opaque plastic insulating tape. The platform was mounted at each end onto a glass ramp (70 mm wide, 150 mm long) that was supported at 45° on a wooden base. One spider was released onto the ramp at each end of the arena and allowed to walk up onto the

platform while an opaque partition was held at the platform mid-point. When both spiders were on the platform, the partition was removed (start of test) so that spiders could see each other and interact. Encounters staged on this arena are referred to as 'in light'. All encounters were video-recorded and assessed later.

In this study I introduce a new class of encounter that has not been explicitly identified in previous studies; 'spectation'. I define spectation as occurring when only one spider sees the other (evident from continued orientation). Spectations may or may not lead to interactions (both spiders see each other). I investigate whether 'spectators' sometimes make use of the apparent opportunity to avoid interactions, or to incite interactions in a particular manner (e.g., display, stalk and attack). Interactions ended when one spider decamped and the other spider did not follow or when a spider left the combined region of arena platform and ramps.

Whether relative size influenced tendency to see the other spider first, tendency to incite interactions and tendency to win contests was determined. A 'loser' ended a contest by decamping, and a 'winner' was the spider remaining at the contest site. Maximum cephalothorax width was used as a measure of spider size. This metric is commonly used for spiders, because cephalothorax dimensions are static within an instar (Hagstrum 1971) whereas measures that include the abdomen (e.g., mass, body length) vary from day to day in relation to feeding and reproductive state. Maximum cephalothorax width was measured to the nearest 0.05 mm using an ocular micrometer while spiders were subdued under carbon dioxide. For encounters involving different classes of individuals (e.g., male-female, male-juvenile), I also determined whether sex or maturity influenced tendency to see the other spider first or tendency to incite or avoid interactions.

Encounters naturally occurring inside rolled-up leaves in darkness

Encounters that would naturally occur in darkness in the cavities of rolled-up leaves were staged inside glass tubes ('dark tubes') under infra-red light in a light-proof cabinet. Salticid eyes are not sensitive to infra-red light (Blest *et al.* 1981; Yamashita 1985; Peaslee & Wilson 1989), so this set-up should have been equivalent to total darkness. The dark tubes were 150 mm long and 10 mm in internal diameter, approximating the dimensions of the rolled-up leaves from which spiders were collected. In nature, rolled-up leaves taper at each end, and spiders inside rolled-up leaves would be able to retreat into these narrow spaces to evade intruders. In the laboratory, a 60 mm-long conical intrusion at one end of the dark tube provided a 'restricted area' into which spiders could retreat to evade each other (Fig. 3). Interactions taking place inside dark tubes were observed using an infra-red video set up inside the light-proof cabinet and connected to a monitor outside.

The two spiders used for encounters staged in dark tubes had different roles. The 'resident' was already in the dark tube when tests began and the 'intruder' was later released into the dark tube to begin tests. For encounters in which the resident was not at a nest, the resident was placed into the dark tube 30 min before testing. For encounters involving residents at nests, residents had continual access to dark tubes for 5-7 days before testing so that nests could be built. To permit a resident access to a dark tube, the open end of the tube (i.e., the end not blocked by the cone) was inserted through a hole in the top of the spider's cage and the tube was then darkened by covering it with an opaque sheath. Spiders usually adopted the dark tube as a resting site.

Thirty minutes before testing, the intruder was placed into a clear plastic 'transfer chamber' (40 mm long, 10 mm internal diameter; Fig. 3) that had a removable opaque partition inserted into a collar at one end. A cork was inserted into the other end to prevent the spider's

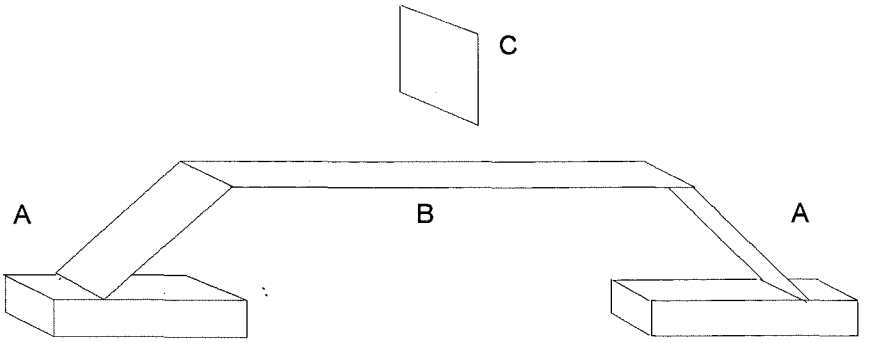

Figure 2. Diagram of testing arena simulating an open flax leaf. (A) ramp and base. (B) Platform. (C) Opaque screen (raised).

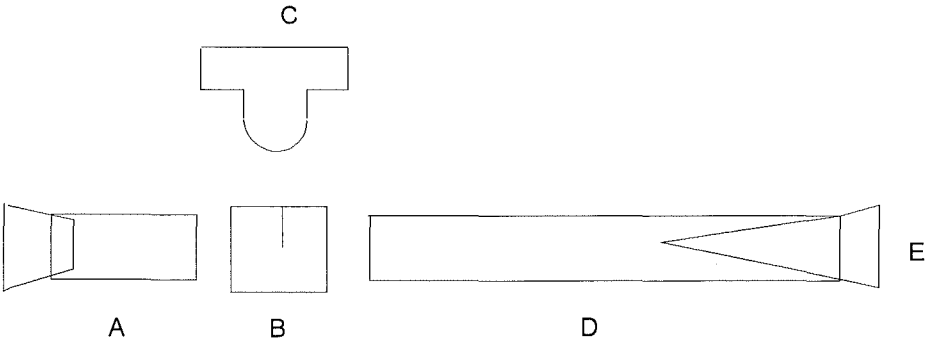

Figure 3. Diagram of testing arena simulating a rolled-up flax leaf. (A) Transfer chamber. (B) Collar holding the transfer chamber to the dark tube. (C) Opaque screen (removed and rotated 90°). (D) Dark tube. (E) Cone inserted into the end of the dark tube to create a 'restricted area'.

escape. The dark tube containing the resident was removed from the resident's cage and the transfer chamber was attached to the open end of the tube by sliding the collar over the dark tube entrance. The partition prevented the two spiders seeing or touching each other. The combined dark tube and transfer chamber was then placed inside the light-proof cabinet. The infra-red video system was turned on and the spiders were left for 30 min to settle down.

To start a test, the partition was removed by reaching through an opaque sleeve (heavy black satin) in the light-proof cabinet using the infra-red video for orientation. Tests began when the intruder left the transfer chamber and entered the dark tube. Once the intruder had moved into the dark tube, the cork in the transfer chamber was carefully removed so that the spiders could exit from the combined dark tube and transfer chamber (end of test). The effects of relative size and residency on outcome of contests in dark tubes were assessed.

Behaviour when entering rolled-up leaves

Behaviour of males and females when entering the cavity within rolled-up leaves was observed using leaves collected in nature. Leaves containing females on nests were collected the day before testing. For both males and females, the resident female was removed for half of the tests. To set up a test, a leaf was clamped onto a laboratory stand so that it angled upward at 45° from the bench (the approximate orientation of these leaves in nature). A test spider was then released at the bottom of the leaf by opening and inverting its cage, allowing the spider to jump onto the leaf. The spider then walked about freely until either entering the cavity within the rolled-up leaf, or departing by walking or jumping off (end of test). Each rolled-up leaf was used only once.

OBSERVATIONS

Morphology and appearance

Trite planiceps adults have dark brown cephalothoraxes and Legs I, and amber Legs II-IV. In both sexes, Legs I are much longer and heavier than the other legs. When viewed from above, the abdomen has a yellow longitudinal band centrally, with a brown stripe on either side. The sides of the abdomen are yellow and the ventral surface is brown. Juveniles resemble females, although their Legs I are not as enlarged or darkened as those of adults, and they have a pale yellow medial stripe on the dorsal carapace. *Trite planiceps* is a moderately sexually dimorphic species, with males differing from females by having a dense row of dark hairs above the anterior median eyes, longer chelicerae and Legs I, and shorter abdomens (in relation to spider size). Most males and females collected from nature were 2.7-3.1 mm in cephalothorax width (8-10 mm body length), but some were as small as 2.4 mm (6 mm body length) or as large as 3.6 mm (14 mm body length).

Locomotion and resting posture

Trite planiceps' usual means of locomotion was to walk, rather than hopping. Although *T. planiceps* adults are capable of jumping more than 150 mm, they tended to jump only when no other route was available or when they had been startled. Spiders usually walked in bursts lasting 1-5 seconds and covering less than 150 mm, pausing frequently as they moved around. Pauses usually lasted only 1-5 seconds, but infrequently lasted as long as one minute as spiders palpated the substrate and looked around.

When resting, most salticids spread their legs outward more or less evenly spaced around their bodies. Whether inside or outside a rolled-up leaf, *T. planiceps* often adopts an unusual resting posture for a salticid; the second and third pairs of legs are tucked in close to

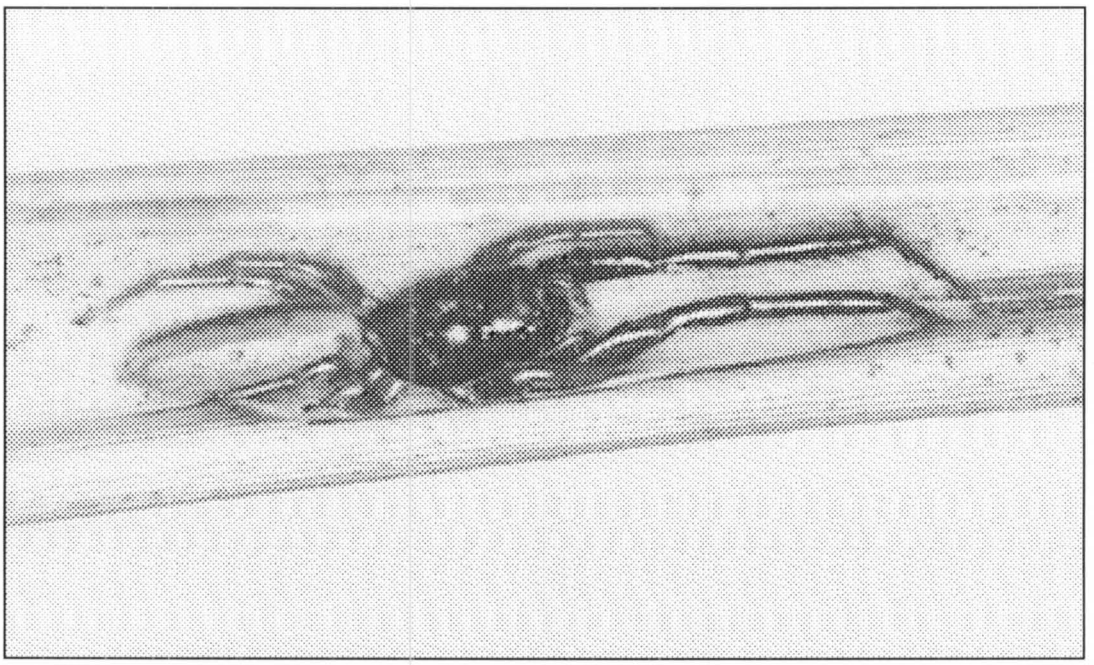

Figure 4. *Trite planiceps* male in the usual resting posture.

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the spider's body, Legs I extend anteriorally and converge, and legs IV extend posteriorally (Fig. 4). When resting, the body is held close to the substrate and the palpal femora are raised and held together so that the distal segments hang together in front of the chelicerae.

Nesting sites and structure of nests

In nature, juveniles, subadults and females were commonly found resting in nests that were built in the dry cavities formed by dead, rolled-up leaves. Nests built by juveniles and subadults were broad, flat enclosing silk cocoons with a door at each end (Fig. 5). These nests were usually c. 1.5 times longer and 2-3 times wider than the resident, and generally resembled nests built by juveniles and subadults of other salticids.

Nests built by adults of most salticids are tube-like cocoons that completely enclose the

resident. Some species additionally build a roof over the cocoon (see Hallas & Jackson 1986a). The nests of *T. planiceps* females are unusual, each instead comprising a silken platform (containing the eggs) and lacking a cocoon enclosing the resident (Fig. 6). In nature, *T. planiceps* females were usually found resting on their nests facing the opening of their rolled-up leaves.

Nests built in the laboratory by females in dark tubes closely resembled nests built in nature. Before ovipositing in the laboratory, females built a thin silken platform approximately 1.5-2 times their own length and width. They then deposited egg-batches, each containing 8-40 eggs, at intervals ranging from one day to many weeks. Each egg-batch was enclosed by its own silken casing, and they were deposited immediately adjacent to, and partly overlapping, older egg-batches (Fig. 6). As many as 7 egg-batches were observed in a single nest in nature, and a nest might simultaneously contain eggs, post-embryos, and first instar juveniles (dispersing stage). If rolled-up leaves were more than c. 10 mm in diameter or had been split open above the nest, females sometimes built silken roofs that descended from the surface opposite the nest. Roofs never touched nests, although the gap between nests and roofs was sometimes just large enough for spiders to pass through.

Except for individuals that had recently moulted (evident from pale colouration), males were only observed in nests in nature or the laboratory when they were cohabiting with subadult females (see Jackson [1986c] for records of cohabitation durations). Nests occupied by cohabiting males were similar to those built by juveniles and subadults, but were sparse and poorly organised, never completely enclosing the spider. Both in nature and in the laboratory, cohabiting males usually were not in nests, but instead simply stood between the subadult female's nest and the leaf (or dark tube) entrance. On five occasions in nature, a different male was found at each end of a subadult female's nest.

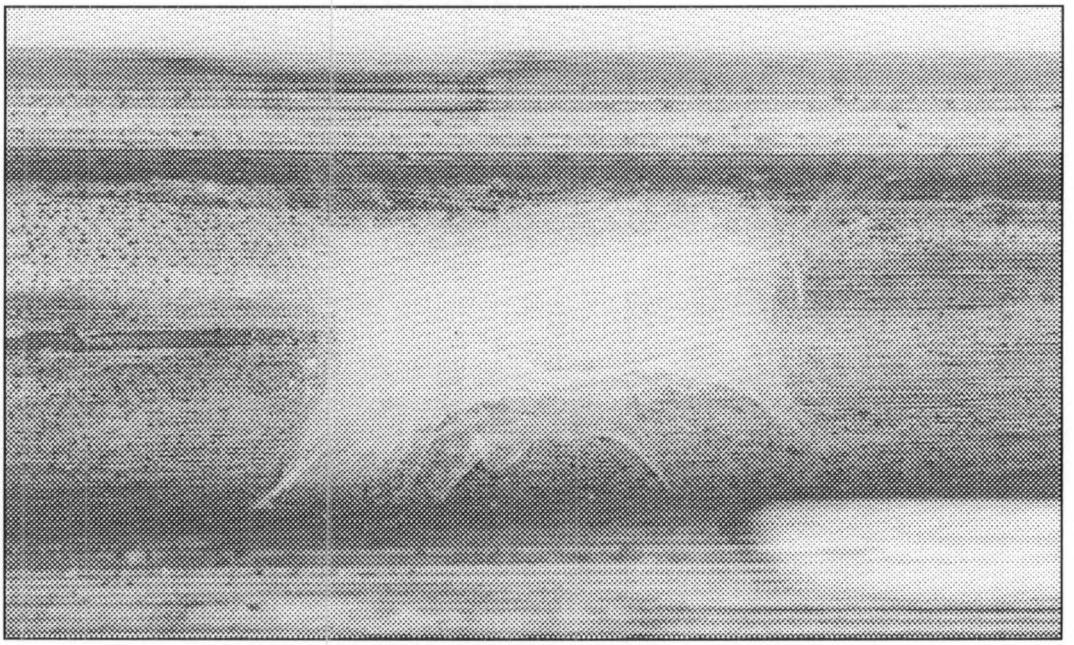


Figure 5. Nest built by a *Trite planiceps* juvenile in the cavity formed by a rolled-up leaf of New Zealand flax.

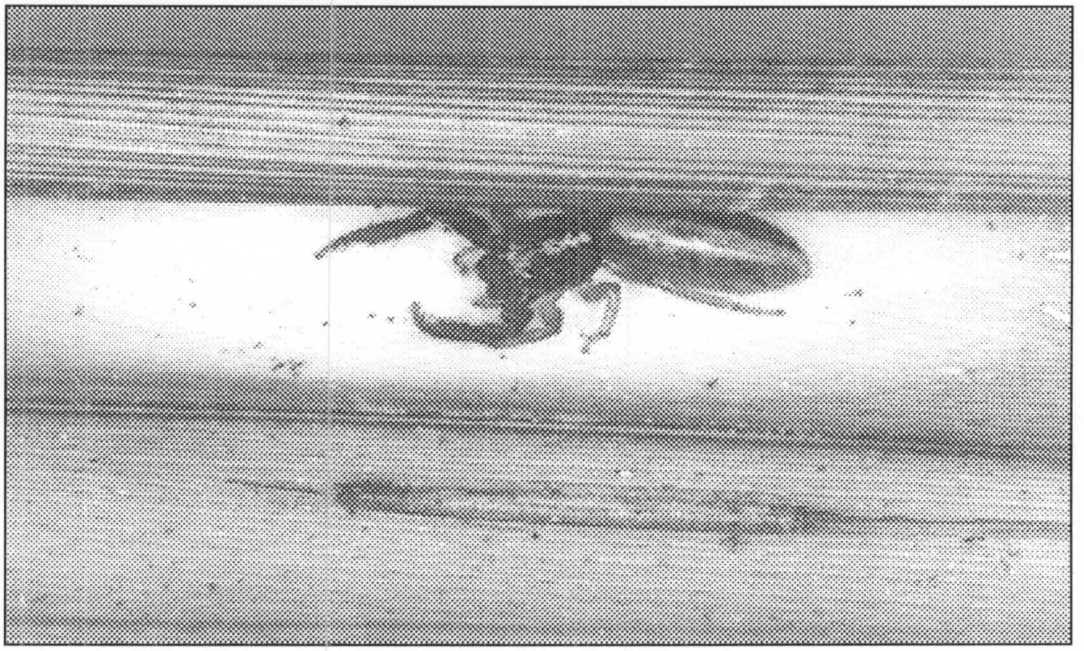


Figure 6. *Trite planiceps* female resting on her nest within the cavity formed by a rolled-up leaf of New Zealand flax.

ELEMENTS OF BEHAVIOUR

Elements of interaction behaviour are described below, and the contexts in which apparent display behaviours were observed are presented in Table 1.

1. Cephalothorax lowered and raised

When walking or standing, the cephalothorax was usually held 1-2 mm above, and parallel to, the substrate. When lowered, however, the sternum touched or was less than 1 mm above the substrate and when raised it was held 2-4 mm above the substrate.

2. Lean and tilt

When standing normally, a spider's legs were all evenly flexed so that the cephalothorax was positioned more or less in the centre of its leg-span, parallel to the substrate. To lean, a spiders flexed its legs, without repositioning the tarsi, so that the cephalothorax was positioned further anteriorally ('leaning forward'), posteriorally ('leaning backward') or to one side ('leaning sideways') than when standing normally. To tilt, a spider either raised the anterior end of the cephalothorax so that it angled as much as 45° up from the posterior end ('tilting upward') or rotated the cephalothorax about its midline by as much as 30° ('tilting sideways').

3. Step sideways

When stepping sideways, one or more tarsi were repositioned no more than once so that the spider moved less than 2 mm to one side. Spiders that stepped sideways usually leaned and tilted sideways in the same direction as the stepping movement.

4. Bent abdomen

When bent, the posterior end of the abdomen was directed as much as 45° to the left or right of the cephalothorax. The posterior end of bent abdomens usually rested on the substrate.

5. Twitch abdomen

A spider twitched its abdomen by rapidly moving it up and down 5-20° from the pedicel (3-8 s^{-1}) in bouts lasting 0.5-3 s. Velocity, amplitude and frequency of twitching usually varied within a single bout.

6. Opened chelicerae and extended fangs

Opened chelicerae were held with the basal segments spread apart. Spiders with opened chelicerae sometimes also extended their fangs. The degree of fang extension was variable, ranging from barely perceptible to full extension (c. 90°). Spiders were never observed to extend their fangs without opening their chelicerae.

7. Palp positions

Normal position The palps were held with the femora close to horizontal and converging slightly, with the rest of the palp hanging straight down anterior to the outer margins of the chelicerae.

Frontal palps The frontal position was similar to normal, except that the femora angled up and converged strongly, almost touching at the patellae. Distal segments hung straight down, obscuring the chelicerae. This position was usually adopted when resting or when stalking prey.

Arched palps Femora of arched palps angled downward and out to the side. From the femur to the tarsus, each palp angled inward so that the tips converged beneath the chelicerae (Fig. 7).

Downward palps Downward palps were positioned straight down alongside the chelicerae, with all joints close to full extension (Fig. 8).

Raised palps Femora of raised palps angled upward close to vertical when viewed from the side, and angling outward slightly when viewed from the front. The rest of the palp angled straight down alongside the femur (Fig. 9).

8. Palpate

To palpate, spiders moved their palps so that their tarsi either repeatedly or continuously touched the substrate. Three distinct patterns of palpating were observed; 'flicking palps', 'sliding palps', and 'up-and-down palpating'. To flick their palps, spiders rapidly moved their palps backward and forward 0.1-0.5 mm, primarily by flexion and extension at the patella. Contact with the substrate was very brief and intervals between flicks were highly variable. Spiders slid their palps by moving them so that their tarsi continuously and smoothly rubbed against the substrate in any direction. When up-and-down palpating, the palps were repeatedly and rapidly raised c. 0.5 mm and lowered onto a nest (2-5 cycles s^{-1}), primarily by flexion at the coxa. Bouts of up-and-down palpating usually lasted 1-3 s and placement of the palps on the silk was forceful so that distinct indentations could be seen in the nest surface. Occasionally, a spider might palpate with only one palp. Phasing was extremely variable for all patterns of palpating, but approximately alternating was most common.

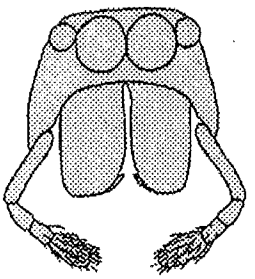


Figure 7. Arched palps.

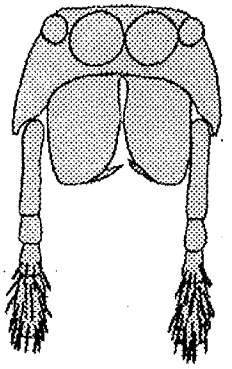


Figure 8. Downward palps.

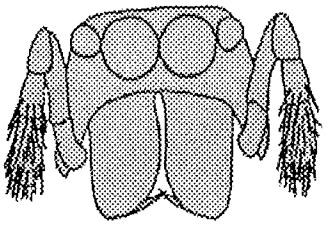


Figure 9. Raised palps.

9. Off-erect legs

When not displaying, *T. planiceps* held Legs I spread less than 20° to the side with all joints flexed slightly and the tarsi resting on the substrate. Off-erect legs were held so that their tarsi were more than 1 mm off the substrate and all joints distal to the femur-patella were close to full extension (Fig. 10). Two distinct patterns of extension were observed at the femur-patella joint. During 'fully extended off-erect legs', the femur-patella joint was within 10° of full extension so that the femur and tibia were in line, and the legs had a stiff appearance along their entire length. During 'loosely extended off-erect legs', the femur-patella joint was flexed more than 10°.

Three modal positions of off-erect legs were observed. 'Type 1 off-erect legs' were fully extended in front of the spider, approximately parallel to each other and the substrate (Fig. 16). 'Type 2 off-erect legs' were spread c. 45° to the side (fully extended or loosely extended) and were angled less than 20° upward (Fig 10). 'Type 3 off-erect legs' were spread c. 45° to the side (usually fully extended) and angled 20-70° upward (Fig. 11).

10. On-erect legs

On-erect legs were like type 2 off-erect legs except that their tarsi were directed downward and their tarsi touched, or were less than 1 mm above, the substrate (Fig. 12). On-erect legs were either fully extended or loosely extended.

11. Forward erect legs

Forward erect legs were similar to type 2 and type 3 off-erect legs ('type 2 and type 3 forward off-erect'), and on-erect legs ('forward on-erect'), except that Legs I were spread only 20-40° to the side. Although forward erect legs were usually either fully or loosely extended,

with flexion primarily at the patella, sometimes joints distal to the patella were also flexed slightly so that the whole leg arched slightly along its entire length.

12. Hunched legs

When hunched, the femora of Legs I angled upward c.45° and were spread c.45° outward from the body midline. The legs were flexed strongly at the femur-patella so that the tibia were directed straight down, perpendicular to the substrate, and the tarsi were flexed so that they converged. The tarsi of hunched legs either touched the substrate, or were less than 1 mm above it. Hunching spiders always had raised cephalothoraxes.

13. Posture

Spiders postured by standing still or walking with Legs I off-erect ('off-erect posturing'), on-erect ('on-erect posturing') or hunched ('hunched posturing'). When posturing with type 2 off-erect legs or on-erect legs, Legs I might be either fully extended or loosely extended.

14. On-erect tapping

To on-erect tap, a spider lifted on-erect legs off the substrate in matching phase (range of lifting 10-70°), and then immediately lowered them back down to on-erect. Males typically completed the upward and downward strokes in 0.1-0.2 s and usually contacted the substrate forcefully with the tarsi, but females usually took 0.5-1 s, and rarely appeared to contact the substrate forcefully. Although spiders sometimes on-erect tapped several times in rapid succession, there was always a distinct pause of at least 0.5 s between on-erect taps.

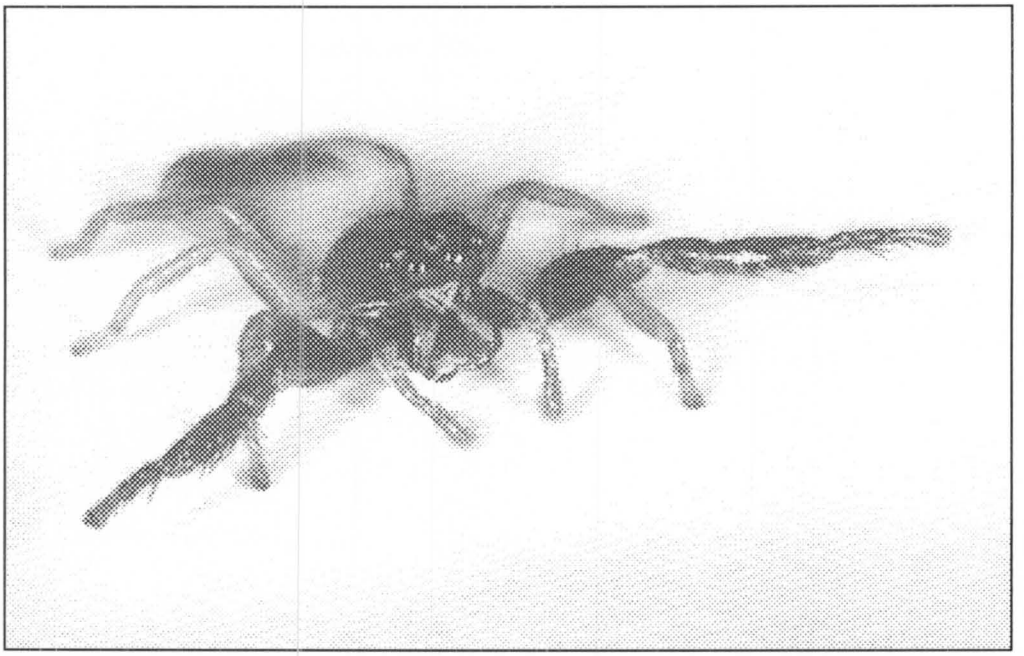


Figure 10. *Trite planiceps* female displaying with loosely-extended type 2 off-erect legs. Cephalothorax is lowered, chelicerae are opened and fangs are extended.

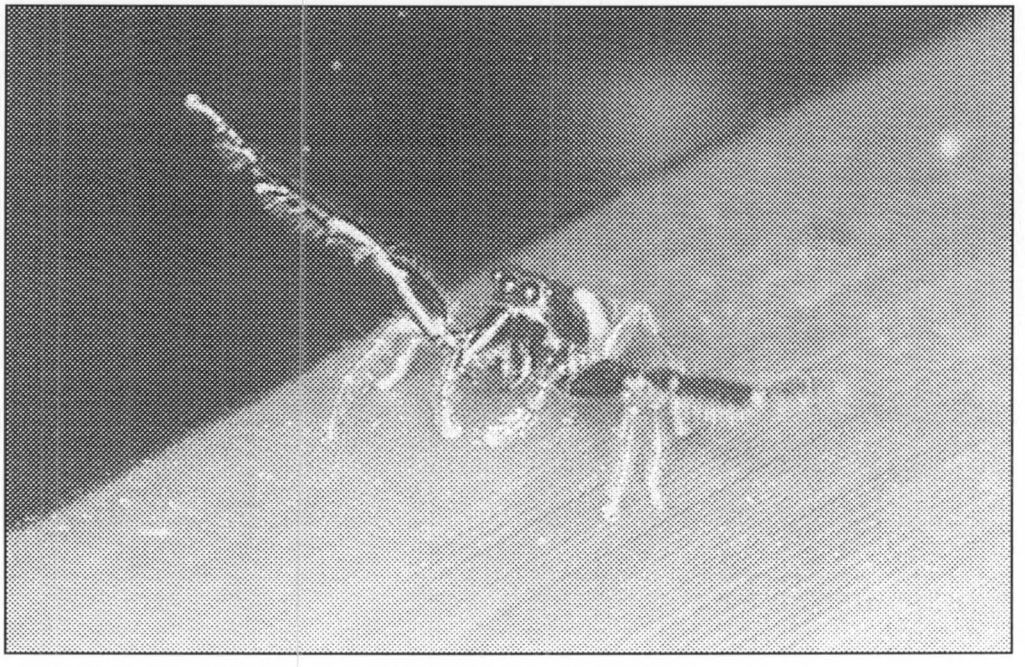


Figure 11. *Trite planiceps* male with type 3 off-erect legs. Chelicerae are open, fangs are extended and the spider is leaning backwards.

15. Forward tapping

To forward tap, a spider lifted Legs I (from the normal walking position, forward on-erect or type 2 forward off-erect) and then immediately lowered them again either onto another spider or the substrate. Flexion was either at the coxa only (tarsi move directly up and down), or at the coxa and patella (tarsi move up and forward, and then directly down). Spiders usually leaned or stepped forward immediately before or while lifting the legs, and then leaned or stepped back again after tapping.

Forward tapping varied in speed, amplitude and forcefulness of contact. However, two general forms of amplitude were most common; 'low forward tapping' and 'high forward tapping'. When low forward tapping the legs were raised and lowered only 10-30°. Low forward tapping could be either slow (0.5-1 s), touching the substrate without force, or fast (c. 0.1 s), touching the substrate with force. When high forward tapping the legs were raised and lowered more than 30°. High forward tapping was always fast and forceful and was usually performed in bouts lasting 2-3 cycles. Phasing was variable, but matching phase was most common for low forward tapping and alternating phase was most common for high forward tapping.

16. Strike

One spider struck another by stepping forward with cephalothorax raised while repeatedly and rapidly raising fully extended Legs I 50-70° and immediately lowering them onto the other spider in alternating phase (2-5 s^{-1}). There was no pause between up and down strokes, and contact with the other spider appeared very forceful.

17. Wave erect legs

From on-erect or type 2 off erect, fully extended Legs I were moved up and down (matching or alternating phase) by flexion at the coxa. The legs remained spread c. 45° to either side and at the highest point, the legs angled 30-60° upward. Spiders often started a bout of waving by raising Legs I in matching phase, then waved them 2-4 times in alternating phase, and finally waved once or twice in matching phase to finish. Males raised and lowered Legs I faster than did females (durations: 0.1 to 0.2 s for males, 0.2 to 1 s for females).

18. Stalk

Spiders sometimes stalked conspecifics in a manner that could not be distinguished from the manner in which flies and other prey were stalked; cephalothorax lowered, palps frontal, Legs I extended straight out in front of the body, and the abdomen raised parallel to the substrate while slowly creeping forward (see Forster 1977a). A stalking spider might 'flicker' by rapidly raising and lowering Legs I from the coxa with no movement at distal joints (alternating phase; c. 4 cycles s^{-1}; c. 2 mm amplitude at the tarsi). As they moved their Legs I up and down, flickering spiders rotated their palps in matching phase but in opposite directions so that the palps were together during the downward part of the cycle of both palps. When stalking flies in their cages, spiders sometimes flickered just before leaping.

19. Oblique walk

Instead of walking directly toward or away from another spider, a spider oblique walked by stepping to one side as it approached or backed away. An oblique walking spider continuously faced the other spider and, when it stopped stepping, usually leaned sideways and sometimes also tilted sideways in the same direction as the stepping movement.

20. Zig-zag dance

A male zig-zag danced by repeatedly oblique walking 5-30 mm to one side, pausing for 0.5-5 s, and then oblique walking 5-30 mm to the other side. The overall effect of zig-zag dancing was to bring the male closer to a female in a series of arcs (although males occasionally zig-zag danced backwards, away from females, during their overall approach).

21. Charge

Spiders charged by suddenly and rapidly running 10-40 mm toward another spider and then stopping abruptly without making contact. Charging spiders usually had raised cephalothoraxes.

22. Long leap

A spider long leaped by jumping 20-80 mm toward another spider, usually contacting the other spider when it landed. Just before long-leaping, the spider positioned its Legs III and IV more in line with the body than during other elements of behaviour, then leaned backwards slightly. Legs I and II were flung rapidly upwards and forwards as the spider extended legs III and IV to leap.

23. Embrace

Embracing spiders stood with their faces touching and their palps raised and extended forward, overlapping those of the other spider (Fig. 13). Embracing spiders usually opened their chelicerae and extended their fangs. Two types of embracing (type 1 and type 2) were observed. When 'type 1 embracing', each spider's Legs I were pressed against the Legs I of the other spider perpendicular to the cephalothorax and approximately parallel to the substrate

(Fig. 13). Type 1 embracing spiders sometimes also pressed Legs II against those of the other spider, but these legs only touched at the tarsi. When 'type 2 embracing', each spider's Legs I were extended forward, loosely draped over the other spider (Fig. 14).

24. Grapple

Embracing spiders grappled by waving fully extended Legs I up and down perpendicular to the cephalothorax midline at highly variable amplitudes (ranging between the substrate and vertical) and rates (2-8 cycles s^{-1}) (Fig. 15). Spiders sometimes grappled with only one Leg I, but if one embracing spider started grappling the other immediately reciprocated with the opposing leg.

25. Hook and push down legs

To hook and push down legs, a grappling spider moved one raised, fully erect, Leg I forward c. 10° from the coxa and then lowered the Leg I straight down to the side so that it contacted the other spider's Leg I, and pushed it downward. The other spider appeared to resist this movement, so that sometimes there was little or no downward movement. A spider sometimes pushed the other spider's Leg I down to the substrate and held it there for c.1 s before they reverted to grappling.

26. Hook and pull

To hook, a spider in a type 2 embrace reached one or both Legs I, and sometimes also Legs II, around the legs, abdomen, or cephalothorax of the other spider (Fig. 14). The hooking spider then pulled by flexing the leg. Sometimes, a hook and pulling spider lifted the other spider's legs off the substrate or pulled the other spider's cephalothorax abruptly forward.

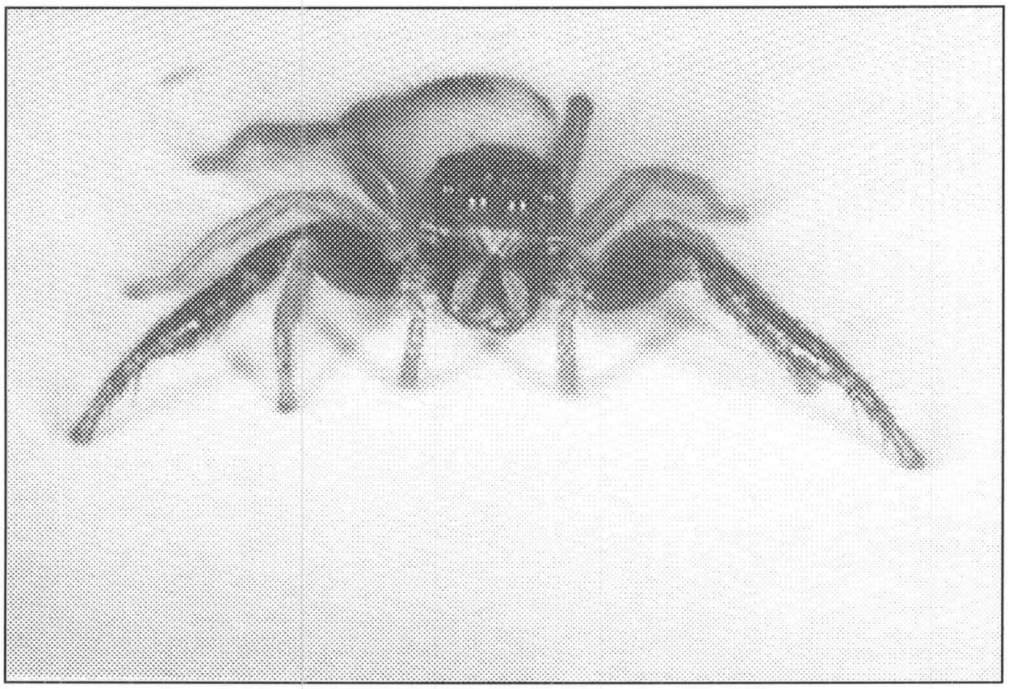


Figure 12. *Trite planiceps* female displaying with loosely-extended on-erect legs

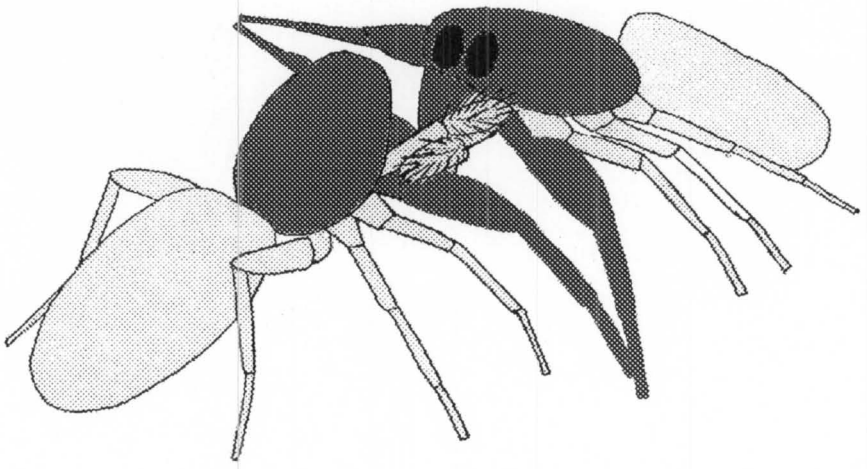


Figure 13. *Trite planiceps* females type 1 embracing.

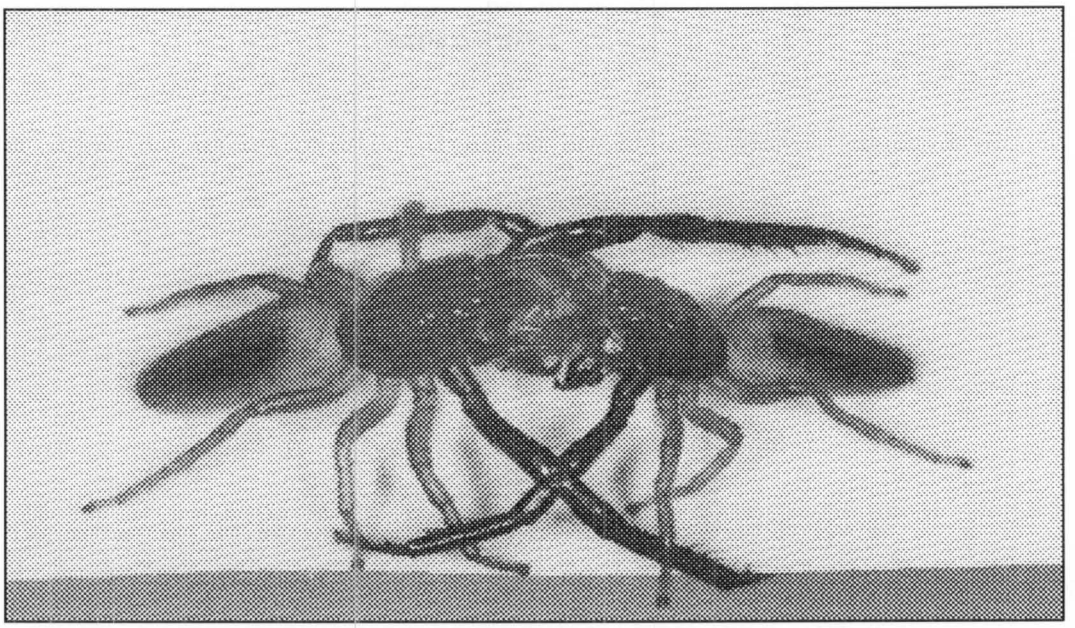


Figure 14. *Trite planiceps* males type 2 embracing. Spider on the right side is hooking and pulling.

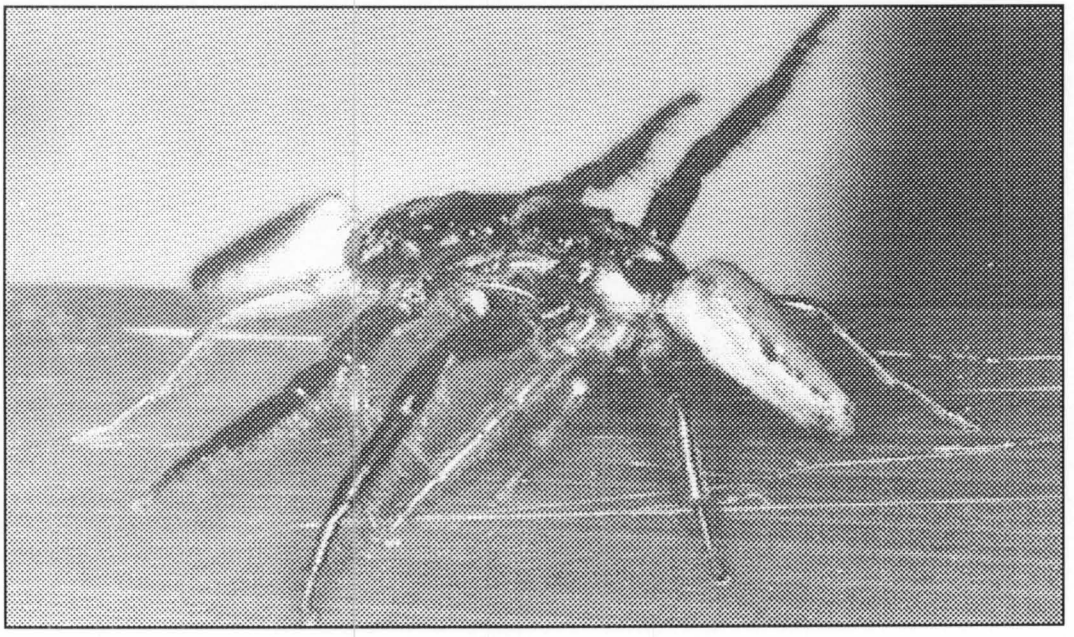


Figure 15. *Trite planiceps* males grappling.

27. Push

Embracing spiders pushed against each other by attempting to step forward. One spider usually managed, apparently against considerable resistance, to force the other to step or slide backwards.

28. Decamp and Retreat

To decamp, one spider walked, jumped or ran away from the other. Retreating was a special type of decamping in which spiders walked backwards so that they faced the other spider while decamping. Retreating spiders usually postured with fully extended type 3 off-erect legs until 80-100 mm from the other spider, and then turned and ran away.

29. Watch and Follow

Spiders watched by turning to maintain orientation toward the other spider. A spider followed by running, walking, or stalking toward a conspecific that was moving away.

30. Lunge and Grab

To lunge, a spider suddenly and abruptly leaned forward 2-4 mm (duration c. 0.1 s) while extending Legs I upwards and forwards. To grab, a lunging spider extended Legs I over another spider while leaning forward and then rapidly flexed Legs I, grasping the other spider. Spiders usually leaned backwards immediately after lunging or lunging and grabbing. If they grabbed, the backward movement was rapid (c. 0.1 s), but if they did not grab the backward movement was usually much slower (c. 0.5 s).

31. Holding lunge

Holding lunges were like ordinary lunges except that the spider kept the tarsi of Legs I on the substrate and always had raised cephalothoraxes. Legs I flexed during the lunge, bringing the spider's face to approximately the position of Tarsi I. Holding lunges were usually repeated two or three times with 1-5 s intervals.

32. Chew and tug

A spider on a nest chewed by inserting its extended fangs into the silk and then opening and closing the chelicerae. Chewing spiders sometimes used their palps to push silk between the chelicerae. A spider tugged by moving its cephalothorax up and down 2-4 mm while gripping the silk with its chelicerae.

33. Probe

With tarsi of Legs I resting on the nest surface, a spider probed by repeatedly (1-2 s^{-1}) pushing and pulling on the silk by moving its Legs I backwards and forwards 1-2 mm, usually in matching phase.

34. Pre-mount tap with legs

A male standing directly in front of a female reached Legs I over the female, lowered the tarsi onto the female's legs, cephalothorax, or abdomen and then repeatedly tapped the female either by moving the whole leg up and down 1-2 mm or, more commonly, by flexing and extending the tarsi (4-6 s^{-1}) . Phasing was extremely variable, but approximately alternating was common.

35. Pre-mount tap with palps

While pre-mount tapping with legs, a male pre-mount tapped with palps by extending his palps forward and repeatedly (2-4 s^{-1}) raising and lowering them c. 1 mm from the coxa so that their tarsi touched the females palps, chelicerae or cephalothorax.

36. Mount

Males mounted by walking onto females (Fig. 16). Usually, the female was facing toward the male when he mounted her, but males occasionally mounted females that were facing to the side or even to the opposite direction. Apparent tactile signals by males after they had mounted are referred to as 'post-mount courtship'.

37. Fend

When a male tried to mount, a female fended by raising one or, more often, both Legs I (loosely or fully extended), preventing the male from mounting. Fending spiders usually tilted their cephalothoraxes upward.

38. Spin

To spin, a spider swept its abdomen from side to side, depositing draglines. Males spun when walking on areas that had been recently walked across by females (female's draglines present), and when mounting. When spinning while walking on areas containing female's draglines, males usually swept their abdomens only once per step, but when spinning while mounting they sometimes swept their abdomens at faster rates.

39. Post-mount tap with legs

After mounting, the male post-mount tapped the female with his legs by placing the tarsi of Legs I on the female's abdomen (Fig. 18) and vibrating the whole leg up and down from the coxa in bouts lasting 0.2-2 s (amplitude 0.1-0.2 mm; velocity 5-10 cycles s^{-1}). The tarsi of tapping legs moved about c. 0.5 mm in all directions across the female's abdomen, but sometimes the legs flexed slightly while tapping, so that the movement of tarsi was mostly toward the male's cephalothorax.

40. Post-mount tap with palps

Males post-mount tapped females with their palps by repeatedly moving them up and down c. 0.5 mm so that their tarsi contacted the female in approximately alternating phase (1-3 cycles s^{-1}). Tapping began on the carapace, and later progressed to the abdomen.

41. Lift leg IV and Rotate abdomen

The male leaned to one side as he tapped the female's abdomen with his palps and legs and the female eventually lifted the Leg IV on that side (Fig. 18). The male then reached Legs I under the female's abdomen, which rotated 45-90° at the pedicel so that the ventral surface was exposed to the male's palp (Fig. 18).

42. Scrape with palps

Once the female's abdomen was rotated, the male scraped the closer palp backward and forward 1-2 mm (2-4 cycles s^{-1}) against the female's ventral abdomen around the genital pores. Palps were usually scraped in bouts lasting 1-10 s, after which there was a pause of 1-10 s before scraping again.

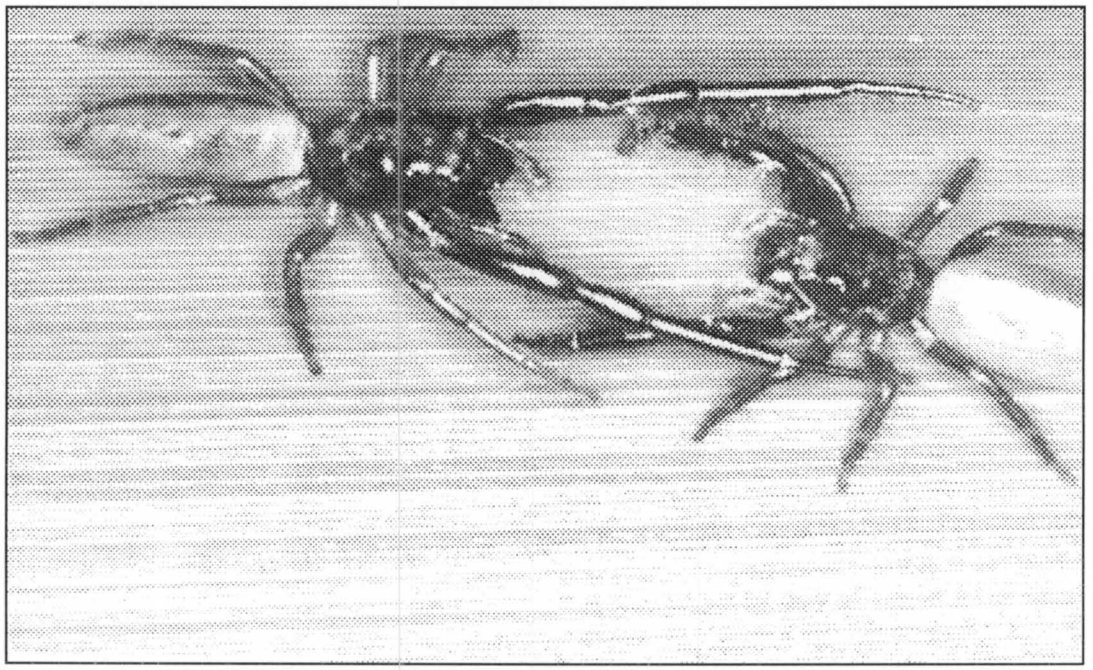


Figure 16. *Trite planiceps* male mounting a female.

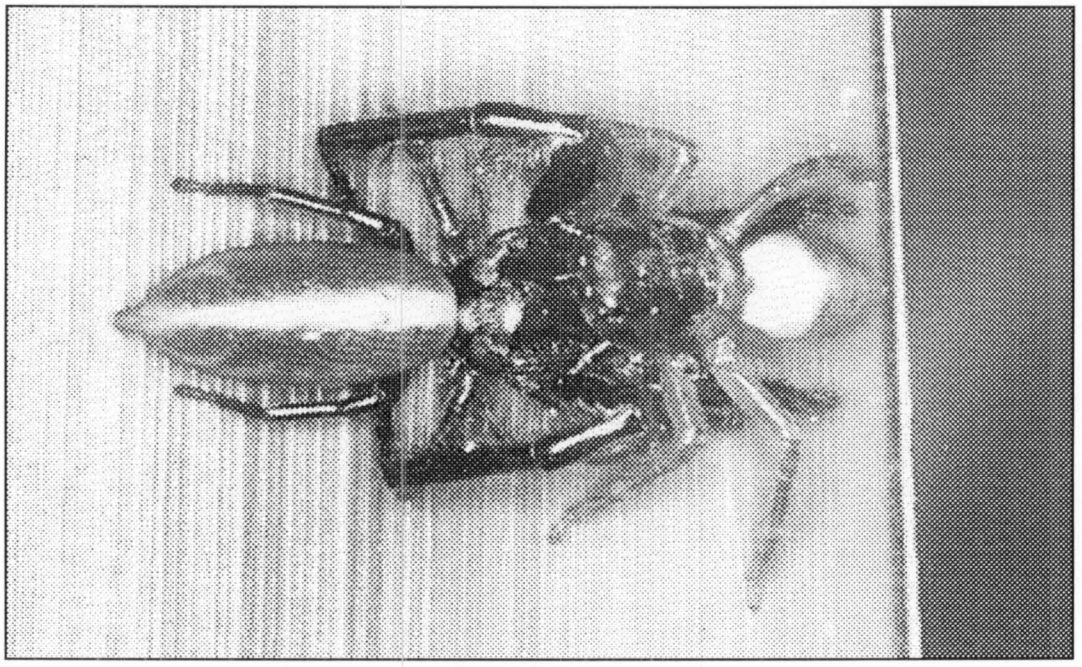


Figure 17. *Trite planiceps* male pausing after mounting a female.

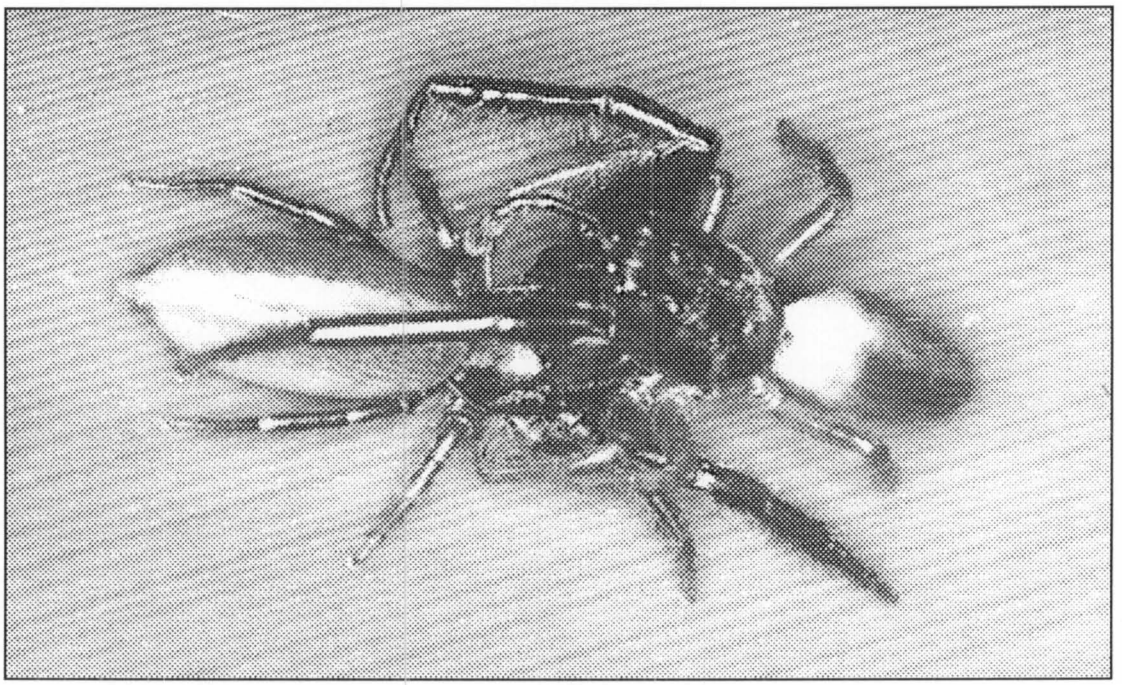


Figure 18. *Trite planiceps* male 'post-mount courting'.

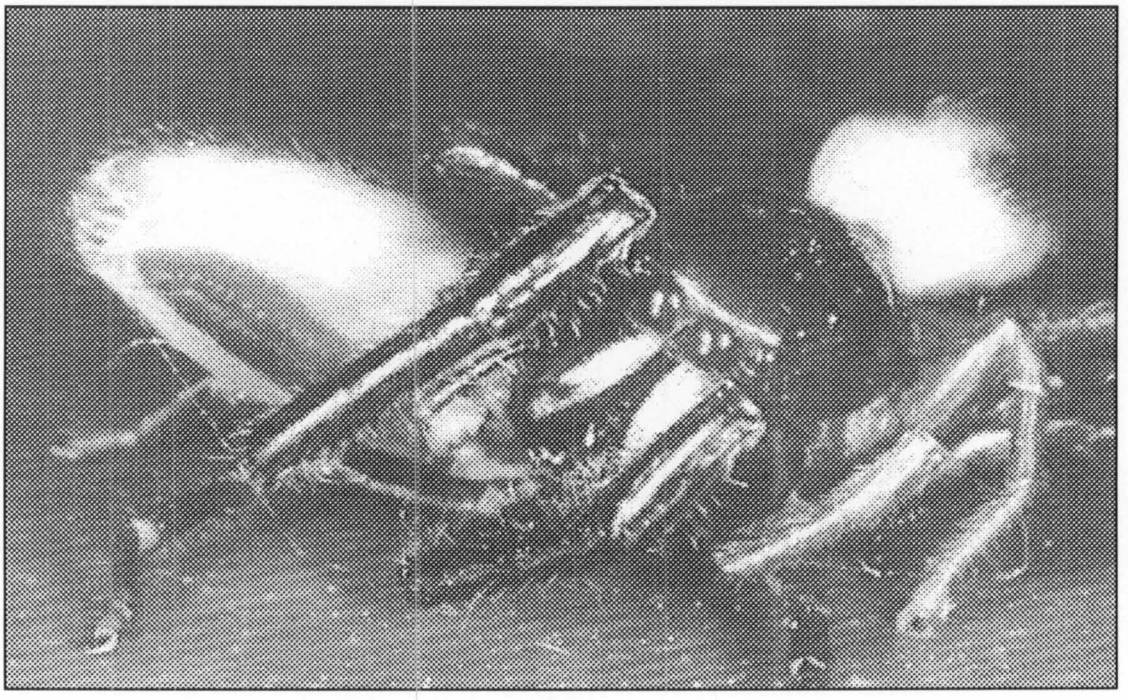


Figure 19. *Trite planiceps* copulating following courtship in light. Female's abdomen is rotated and her Leg IV is lifted.

Table 1. Elements of behaviour used by *Trite planiceps* adults during intraspecific interactions in the laboratory, and the types of interactions during which they were observed (L = in light; T = inside dark tubes; X = not observed)

	Male-female	Female-male	Male-male	Female-female
Bent abdomen	X	L	X	L
Charge	X	L	L	L
Embrace				
type 1	L	L	L	L
type 2	X	X	L	X
Flicker	X	L	X	L
Forward tapping	T	T	T	T
Forward off-erect legs				
position 2	T	T	T	T
position 3	T	T	T	T
Forward on-erect legs	T	T	T	T
Grapple	X	X	L	X
Holding lunge	X	T	X	T
Hook and push down legs	X	X	L	X
Hook and pull	X	X	L	X
Hunched legs	X	L	X	L
Lean	L/T	L/T	L/T	L/T
Long leap	X	L	L	L
Oblique walk	L	L	L	L
Off-erect legs				
position 1	L/T	X	X	X
position 2	L	L	L	L
position 3	L	X	L	L
On-erect legs	L	L	L	L
On-erect tapping	L	L	L	L
Open chelicerae	L/T	L/T	L/T	L/T
Up and down palpating	T	X	X	X
Palps arched	X	L	L	L
Palps downward	L	L	X	X
Palps frontal	X	L	L	L
Palps raised	T	T	T	T
Post-mount tap with legs	L/T	X	X	X
Post-mount tap with palps	L/T	X	X	X
Pre-mount tap with legs	T	X	X	X
Pre-mount tap with palps	T	X	X	X
Scrape palps	L/T	X	X	X
Stalk	X	L	L	L
Strike	X	L/T	L	L
Step sideways	L	L	L	L
Tilt	L/T	L/T	L/T	L/T
Twitch abdomen	L/T	T	L/T	T
Wave erect legs	L	L	L	L
Zig-zag dance	L	X	X	X

43. Apply palp

The male's palp was referred to as applied when the palpal organ was positioned on the female's genital pore and scraping ceased. The haematodocha repeatedly inflated and deflated while the palp was applied, and presumably the embolus was inserted during this time.

Copulation was defined as the period during which palps were applied, not including the latency between applications. *Trite planiceps* adopted the usual copulatory position of salticid spiders (Fig. 19) with the two spiders facing opposite directions and the male's ventral surface against the female's dorsal surface (Gerhardt & Kaestner 1937).

ORGANISATION OF BEHAVIOUR

Sequences of behaviour during spectations and interactions were extremely variable, and only general trends are described. Interaction durations are presented in Table 2.

Table 2. Durations of intraspecific interactions of *Trite planiceps* in the laboratory. Copulation is excluded from male-female interactions.

	Male-female (female receptive)	Male -female (female unreceptive	Male-male	Female-female
i) in light				
Number of tests	-	-	64	77
Number of spectations	-	-	10	19
Number of interactions	17	43	52	52
Maximum interaction duration	5.01 min	3.33 min	1.13 min	73.35 min
Minimum interaction duration	70 s	1 s	1 s	1 s
Median interaction duration	142	49 s	18 s	34 s
ii) in dark tubes				
Number of tests	28	33	20	20
Number of interactions	27	33	20	20
Maximum interaction duration	91.38 min	59.43 min	29.42 min	47.05 min
Minimum interaction duration	4 s	57 s	9 s	1 s
Median interaction duration	1.22 min	4.36 min	1.47 min	24s

Male-female interactions in light

Males were generally more active than females, and were prone to precluding interactions by walking off the arena before seeing the female, or by running quickly toward the female (without seeing her) causing her to flee. For tests using virgin females, females tended to see males first (N = 40, Binomial test, $P < 0.05$), but interaction more frequently ensued when males saw females first (test of independence, $X^2 = 4.98$, $P < 0.05$).

If the male was facing away, virgin females sometimes stood still, watching the male move about, but infrequently stalked or walked towards the male while waving erect legs or tapping on-erect legs. If males oriented to face them, virgin females usually stopped approaching. For tests using mated females, there was no evidence that males or females tended to see the other first (N = 36, Binomial test, $P > 0.5$) and there was also no evidence that likelihood of interaction depended on which spider saw the other first (test of independence, $X^2 = 1.13$, $P > 0.2$). Compared with virgins, mated females were more prone to charging or stalking and then long leaping at males that had not seen them, rather than standing still or drawing the male's attention by waving erect legs or tapping on-erect legs. Irrespective of whether the female was virgin or mated, or what direction she was facing, males that saw females usually displayed immediately and approached.

Males zig-zag danced toward females while waving erect legs, either leaning or leaning and tilting sideways at the end of each bout of stepping. When a male was more than 80 mm away from the female, he usually postured with Legs I loosely on-erect after a bout of waving but when closer to the female he more often postured with Legs I fully extended on-erect or type 2 off-erect (sometimes with Legs I in different postures). Males usually twitched their abdomens immediately before each bout of waving and held their palps downward throughout their approach.

Females sometimes decamped around the edge of the platform to the opposite surface as males approached them. Males then sometimes postured with loosely on-erect legs and intermittently tapped on-erect legs, sometimes for as long as 30 s after females moved out of sight. More frequently, males followed females to the opposite surface of the platform and then looked around, apparently searching for them. If they failed to find the departed females, males sometimes moved repeatedly from one surface to the other for as long as several minutes, looking around on both the upper and lower surface. Both males and females appeared to detect each other's movements when on opposite sides of the platform; if the other spider walked near them on the other surface, spiders often raised their cephalothoraxes and remained very still, and females sometimes ran away immediately after males passed beneath them in the opposite direction.

As males approached them, mated females usually either charged with raised cephalothoraxes and bent abdomens and then long leaped, or ran away. Mated females occasionally tapped on-erect legs and waved erect legs as they charged. Although virgin females sometimes charged with raised cephalothoraxes, they rarely long leaped at males. When females charged or long leaped at them, males sometimes raised Legs I to type 3 off-erect, leaned backwards and tilted their cephalothoraxes upward, and occasionally retreated.

When they were within c. 15 mm of females, males, with legs type 1 off-erect, stepped forward to mount (Fig. 16). Mated females kept their cephalothoraxes raised, bent their abdomens, fended and struck, or decamped, never allowing males to mount. Mated females usually opened their chelicerae and extended their fangs while facing males that attempted to mount. In one instance, a type 1 embrace was observed between a mated female and a male that was attempting to mount her. The spiders pushed against each other with chelicerae open and fangs extended in a manner that could not be distinguished from embraces between two

females. After c. 5 min, the female was pushed backwards and the male immediately attempted to mount. The female then fended and struck, and eventually jumped off the platform.

Virgin females usually fended and sometimes decamped as males were trying to mount. When females decamped, males usually followed and continued courting. Some females eventually stopped fending and lowered their cephalothoraxes, allowing males to mount. While mounting, males sometimes spun, depositing silk over the female's Legs I. Once they were positioned with their palps resting near the female's pedicel and tarsi of highly flexed Legs I resting on either side of the female's abdomen, males usually paused for 10-20 s before beginning post-mount courtship (Fig. 17).

During post-mount courtship, males initially post-mount tapped the female's abdomen with their palps and legs while slowly leaning to one side of the female's midline, and intermittently twitched their abdomens. Males sometimes paused for 10-30s during post-mount courtship, but always began courting again after females began flexing and extending all their legs slightly, and raising Legs I so that they pressed against the males ventral abdomen. Eventually, the female raised Leg IV on the side to which the male was leaning and the male leaned further over, reaching his outermost Leg I under the female's abdomen (Fig. 16). The male then continued to tap with palps and with the other leg for 10-30 s until both his Legs I 'cradled' the female's abdomen (Fig 17), which was now rotated. Males then switched from tapping with palps to scraping with palps and eventually applied the closer palp and copulated.

While copulating, the spider's bodies pulsed gently from side to side in phase with the expansion and retraction of the haematodocha. Pulses were usually 2-6 s apart, but often were irregular and less frequent near to the end of a palp application. Between palp applications, males usually returned to the female's midline and paused in the same position as during the

pause following mounting. They then leaned to the other side, tapped with legs and palps again, and eventually applied the second palp.

Mating ended either when the male withdrew his palp and dismounted or when the female became active, dislodging the male. Once males were dismounted, females usually opened their chelicerae, extended fangs, and raised Legs I to type 3 off-erect. Females sometimes raised their cephalothoraxes, bent their abdomens, and then charged at and struck males. Males that had copulated without interruption using both palps decamped readily. However, if males had not copulated with both palps, they usually began courting again.

Male-male interactions in light

Smaller males tended to see larger males first (N = 64, Binomial test, $P < 0.001$), but there was no evidence that likelihood of interaction depended on which spider saw other first (test of independence, $X^2 = 0.82$, $P > 0.3$). A male that saw another male, but was itself undetected, usually arched its palps, and then waved erect legs or tapped on-erect legs while charging or oblique walking toward the other spider, causing it to orient. Other interactions began when the spiders faced each other more or less simultaneously, arched their palps, and postured with on-erect or type 2 off-erect legs. Males rarely stalked or long leaped at other males.

The spiders then charged or oblique walked toward each other. When not moving toward its rival, a spider sometimes stepped sideways. Spiders usually tapped on-erect legs while charging or oblique walking, and postured (on-erect or type 2 off-erect) or tapped on-erect legs while stepping sideways. Usually, following oblique walking or stepping sideways, spiders leaned or leaned and tilted in the direction of movement. Between bouts of stepping, spiders usually postured with on-erect legs or type 2 off-erect legs, sometimes with one Leg I

in each position (especially if leaning). Males often twitched their abdomens immediately before a bout of stepping.

When they were less than two body lengths apart and facing each other, the spiders might initiate an embrace (type 1 or type 2) by stepping forward until their chelicerae touched and their palps were raised and overlapping. Embracing spiders usually grappled and then hooked and pushed down legs. Type 2 embracing spiders usually hooked and pulled, and occasionally lunged and attempted to bite each other. Following an embrace, the winner usually ran or long leaped after the decamping loser. Larger males won 44 of 53 contests that were asymmetric for size (Binomial test, $P < 0.001$). No injuries occured during encounters between males.

Female-female interactions in light

Smaller females tended to see larger females first (N = 77, Binomial test, $P < 0.005$), but there was no evidence that likelihood of interaction depended on which spider saw the other first (test of independence, $X^2 = 1.15$, $P > 0.2$). When they saw another female, but were themselves undetected, females might stand still and watch the other spider, or they might approach the other spider by stalking, long leaping, or charging with cephalothorax raised and abdomen bent. Charging spiders sometimes waved erect legs or tapped on-erect legs. Two instances of cannibalism were observed immediately following spectations. In one, a female stalked and then long leaped, grasping the other spider as it oriented, and then began to retreat with Legs I type 3 off-erect. In the other instance, the spectator stood still, undetected, as the other spider approached, and then simply lunged and grabbed the victim as it walked by.

During interactions, the two females usually took distinctly different roles. One female arched its palps, postured (usually on-erect or type 2 off-erect, rarely hunched), waved erect

legs and tapped on-erect legs while the other spider stalked (palps frontal) or raised its cephalothorax and bent its abdomen (palps arched). One of the spiders then charged and might long-leap while the other spider stood still, watching. Spiders that were charged or long leaped at sometimes raised Legs I to type 3 off-erect, leaned backwards and tilted upwards, or retreated. Winners usually chased after decamping losers, and occasionally long leaped or struck them. Sometimes, when a long leaping spider landed, the spiders grasped onto each other with Legs I and then rolled off the platform struggling and attempting to bite each other. Females rarely embraced, but embraces between females tended to be much longer than embraces between males (males N = 7, range 1-29 s; females N = 3, range 21-73 min). Larger females won 43 of 54 contests that were asymmetric for size (Binomial test, $P < 0.001$).

Interactions between adults and subadult females in light

Subadult females tended to see adult females first (N = 40, Binomial test, $P < 0.001$) but interaction more frequently ensued if the adult female saw the subadult female first (test of independence, $X^2 = 10.00$, $P < 0.005$); subadult females that saw adult females tended to avoid detection by lowering their cephalothoraxes and remaining still, or decamping. Interactions between subadult females and adult females were generally similar to interactions between two adult females. One spider, usually the adult, charged and oblique walked toward the other spider while posturing (on-erect or type 2 off-erect) and tapping on-erect legs or waving erect legs, while the other spider watched, stalked, or charged with cephalothorax raised and abdomen bent. Females and subadult females sometimes long leaped at each other. Adult females won 16 of 20 contests with subadult females (Binomial test, $P < 0.001$). Winners were always larger than losers and no injuries occured.

Subadult females tended to see males first (N = 35, Binomial test, $P < 0.001$), but

interaction more frequently ensued if the male saw the subadult female first (test of independence, $X^2 = 6.81$, $P < 0.01$). Subadult females occasionally charged and waved erect legs at males that had not seen them, but more frequently remained still and ran away when males approached them. Immediately after seeing subadult females, males began courting as though the subadults were adult females. Subadult females sometimes raised their cephalothoraxes and charged at males that were courting them, and infrequently long leaped and then immediately ran away. If subadult females failed to decamp, males always tried to mount them. Subadult females prevented males from mounting by fending and tilting their cephalothoraxes upward. Although subadult females sometimes decamped as males tried to mount, they usually did not move more than 50 mm before stopping. Males usually followed them, courting and attempting to mount several times before the subadult females walked or jumped off the platform or males failed to follow.

Interactions involving juveniles in light

Smaller juveniles tended to see larger juveniles first (N = 44, Binomial test, $P < 0.001$) but interaction more frequently ensued when the larger spider saw the smaller spider first (test of independence, $X^2 = 6.29$, $P < 0.05$). Juveniles occasionally stalked and long leaped at other juveniles that had not seen them. In one instance, a long leaping juvenile captured and killed the other juvenile. Interactions were similar to contests between adult females; one juvenile usually postured (on-erect or type 2 off-erect), tapped on-erect legs, and waved erect legs, while the other raised its cephalothorax and bent its abdomen. Both juveniles usually arched their palps. Interactions usually ended immediately after one spider charged and long leaped and the other spider decamped. Larger juveniles won 22 of 26 contests that were asymmetric for size (Binomial test, $P < 0.001$).

Juveniles tended to see females first (N = 36, Binomial test, $P < 0.001$) but interaction more frequently ensued when the female saw the juvenile first (test of independence, $X^2 = 31.75$, $P < 0.001$). Juveniles that were undetected usually avoided interactions with females by lowering their cephalothoraxes and remaining still, or running away before being seen. Juveniles never displayed at females and usually decamped within 10 s after interactions began. Females sometimes charged, waved erect legs and long leaped at juveniles that were oriented toward them or facing away from them. In one instance, a long-leaping female captured and killed a juvenile.

Juveniles tended to see males first (N = 36, Binomial test, $P < 0.005$) but interaction more frequently ensued when the male saw the juvenile first (test of independence, $X^2 = 24.08$, $P < 0.001$). Juveniles rarely approached males, instead either lowering the cephalothoraxes and standing still, or immediately running away. When they saw juveniles, males behaved basically as they did after seeing adult or subadult females; zig-zag dancing, waving erect legs, and posturing with on-erect and type 2 off erect legs as they approached with palps downward. Juveniles usually ran away after standing still and watching males for less than 10 s, but they occasionally charged with cephalothorax raised, or long leaped (rare), before running away.

Male-female interactions in dark tubes

While walking along dark tubes toward females males usually flicked their palps, twitched their abdomens, forward tapped (high or low, with or without force) and sometimes spun. When a male stepped onto a nest, forward tapping was only low and without force. Females, apparently alerted by nest-bound vibrations from as far as 25 mm away, sometimes walked towards males that touched their nests. If females did not approach them, males palpated (flicking, sliding, and up and down), chewed and tugged, and probed.

When touched by males, females raised their palps, opened their chelicerae, raised legs to type 2 or type 3 forward off-erect, leaned backwards, and tilted their cephalothoraxes upwards. Females sometimes then lowered their Tarsi I back down to the substrate, raised their cephalothoraxes, twitched their abdomens and holding lunged. Mated females not on nests sometimes lunged and grabbed, but virgin females and mated females on nests only rarely lunged. On one occasion, a lunging female (mated, away from nest) caught and killed a male.

Males repeatedly low forward tapped or stepped forward and touched females with type 2 forward off-erect legs or type 1 off-erect legs, and then attempted to mount. Females, especially if virgins or if at nests, sometimes lowered their bodies and allowed males to mount after fending for less than 2 min. Alternatively, females (especially if mated and not on a nest) retreated to the restricted area. At first, males followed and attempted to mount, but they soon switched to pre-mount tapping with legs and palps. After as long as 40 min of pre-mount tapping with legs and palps, females walked forward out of the restricted area and males immediately mounted. Mounting, post-mount courtship and copulation were similar to observations in light. Mated females more frequently mated when nests were present (12 of 14) than when nests were not present (6 of 15) (test of independence, $X^2 = 6.43$, $P < 0.05$). Virgin females always mated when they encountered males inside dark tubes (N = 17, all away from nests).

Male-subadult female interactions at nests in dark tubes

Males approached subadult females in the same manner as when approaching adult females. If the subadult female was in a nest and did not approach the male when he touched the silk, the male up and down palpated, chewed and tugged, and probed. Immediately after they touched males, subadult females usually leaned backwards and raised Legs I to type 2 or

type 3 forward off-erect, or raised their cephalothoraxes. Subadult females sometimes forward tapped (high or low), opened their chelicerae, and extended their fangs. When hit by forward-tapping subadult females, males usually leaned backwards and raised Legs I to type 3 forward off-erect.

Instead of mounting, males only briefly premount tapped with legs and palps, twitched their abdomens, and then backed away. Males usually then turned around to face the dark tube entrance and remained in that position until recording ended 1 h later. Subadult females sometimes approached and touched males, causing them to orient. These later encounters were always very brief, ending either when males turned and faced away from the subadult again or when subadult females returned to their nests.

Male-male interactions in dark tubes

Intruders twitched their abdomens, flicked their palps and forward tapped (high or low) as they walked toward residents. Usually, there there were no noticeable responses by residents until the spiders touched each other. When they touched for the first time, spiders usually leaned backwards, tilted their cephalothoraxes upwards, raised Legs I to type 3 forward off-erect, raised their palps, opened their chelicerae and extended their fangs.

Interactions between males sometimes appeared very 'cautious'. The spiders often twitched their abdomens, and then slowly leaned forward, low forward tapped or touched the other spider or the substrate without tapping, and then leaned back again. The other spider sometimes leaned backwards immediately after one spider low forward tapped, even when the tapping spider touched the substrate and not the other spider. If one forward tapping male touched the other male, the touched male sometimes raised Legs I to type 3 forward off-erect and tilted its cephalothorax upwards as it leaned backwards. Spiders sometimes stood still,

facing one another from 5-20 mm away with legs loosely extended forward on-erect or loosely extended type 2 forward off-erect for as long as 1 min. Occasionally, when standing still, spiders draped Legs I loosely over each other, and might pull gently at each others appendages by flexing and extending the tarsi. Palps were always held in the raised position during these exchanges.

Males facing one another sometimes took turns at high forward tapping, with an interval of 0.5-2 s between turns ('reciprocal high forward tapping'). During these exchanges, a spider leaned forward or stepped forward 1-2 paces, high forward tapped very forcefully 2-3 times in alternating phase, and then leaned or stepped back to its original position. The other spider then reciprocated.

Residents sometimes retreated to the restricted area and the intruder usually then pushed up against the resident. The resident usually kept its Legs I type 3 forward off-erect, and the intruder usually draped Legs I loosely over the resident, and sometimes gently pulled at the resident by flexing and extending Legs I. Residents sometimes then stepped sideways around the tube, walked past the intruder and left the tube. Both relative size and residency were good predictors of outcome for contests between males in dark tubes (Table 3: tests of independence; relative size, $X^2 = 12.10$, $P < 0.001$; residency, $X^2 = 6.40$, $P < 0.05$). Males rarely lunged at each other, and no injuries were observed during male-male interactions.

Female-female interactions in dark tubes

As females walked along dark tubes, they very gently low forward tapped and palpated (flicking and sliding). When they touched a conspecific's nest, intruders might up and down palpate. If no nest was present, females did not appear to respond to each other until they touched, but if a nest was present the resident appeared to be alerted to the intruders presence

from as far as 25 mm away, walking quickly toward the intruder.

When they touched, both females usually immediately leaned backwards, tilted their cephalothoraxes upwards, raised their palps, opened their chelicerae, and raised Legs I to type 2 or type 3 forward off-erect. After a few seconds, one or both spiders might lower its Legs I to normal or loosely extended forward on-erect and raise its cephalothorax. Females with raised cephalothoraxes sometimes holding lunged and twitched their abdomens.

Residents sometimes lunged and grabbed at intruders and intruders sometimes then immediately retreated and decamped from the tube. Alternatively, residents sometimes retreated to the restricted area, and the intruder usually followed and then stepped forward so that its Legs I extended over the resident. Residents initially kept Legs I type 3 forward off erect, but then usually lowered their Legs I onto the intruder so that the two spiders stood face to face with their Legs I loosely draped over one another. They then remained almost motionless for as long as 20 min before the intruder retreated and left the tube. If they remained away from the restricted area, spiders sometimes stood 5-20 mm apart, facing each other, with legs normal, loosely extended forward on-erect or type 2 off-erect, and intermittently low tapped without force.

Losers usually retreated away from winners until they reached the tube opening, and then stepped out of tubes backwards, turned and walked away as soon as they were outside. Residents tended to win contests (Table 3, test of independence, $X^2 = 25.60$, $P < 0.001$), but relative size did not appear to influence contest outcome (Table 3, test of independence, $X^2 = 0.00$, $P = 1.00$). The only injury observed was when an intruder lunged, caught, and killed a much smaller resident immediately after they first touched.

Table 3. Relationship between Residence, Relative size and Outcome of contests between adult *Trite planiceps* inside dark tubes. Numbers indicate how many of 20 male-male and 20 female-female contests were won by each of the four possible classes of victor (intruders were larger in 10 tests, and smaller in the other 10 tests for both males and females)

Contest winner	Male-Male	Female-Female
Larger resident	10	9
Smaller resident	4	9
Larger intruder	6	1
Smaller intruder	0	1

Effects of reproductive state and interaction site on mating

Matings involving mated females (in dark tubes only) entailed more palp applications than matings involving virgins in light or in dark tubes (Table 4, Mann-Whitney U test, both comparisons $P < 0.001$). Males applied their palps for shorter durations each time when mating with mated females (in dark tubes) rather than virgin females (in light or dark tubes) (Table 5, Mann-Whitney U test, both comparisons $P < 0.001$). Also, males applied their palps for shorter durations each time when mating with virgins in light rather than in dark tubes (Table 5, Mann-Whitney U test, $P < 0.001$).

Total copulations durations (sum of palp application durations) were shorter for virgin females in light than for virgins in dark tubes (Table 6, Mann-Whitney U test, $P < 0.001$) but total copulation duration was similar for mated females and virgins in dark tubes (Table 6, Mann-Whitney U test, $P > 0.3$). Distinctive white deposits were always present in female's genital pores after mating and similar deposits were often observed in the genital pores of adult females in nature (Fig. 20).

Behaviour of spiders on rolled-up leaves occupied by females

The behaviour of both males and females was similar on leaves with and without the resident female present. Males found the openings of rolled-up leaves in 18 of 20 tests. Before finding the openings, males moved frequently and rapidly in bursts lasting 0.1-0.5 s, broken by pauses of 1-15 s. Males palpated the leaf surface whenever they stopped (flicking and sliding palps), and occasionally spun. After seeing openings, males sometimes on-erect postured, tapped on-erect legs, and twitched their abdomens while walking towards the opening. When they reached the opening, males usually leaned forward into the cavity with legs forward on-erect or forward type 2 off-erect, forward tapped (high or low), and repeatedly twitched their abdomens before stepping inside. Males then usually turned through 90° several times, forward tapping in both directions just inside the cavity, before walking further in. Scuffling sounds were heard soon after males entered leaves containing females, and males always soon after retreated out of the cavities with Legs I type 3 off-erect and continued decamping once outside. In each case, the female was seen at the opening immediately after the male departed. In one test, the female stepped out of the opening and onto the outside surface of the rolled-up leaf as the male approached the opening. The female long-leaped at the male, and then ran back inside. The male immediately followed the female through the opening into the cavity within the rolled-up leaf.

Females did not display as they approached the openings of rolled-up leaves (N = 17; 3 failed to find the opening), but they did usually turn through 90° several times, repeatedly low forward tapped, and twitched their abdomens while entering and immdiately after entering the cavity.

Table 4. Number of palp applications during copulations involving virgin and mated *Trite planiceps* females in light and in dark tubes. No copulations were observed for mated females in light.

	Virgin females		Mated females
	light	dark tubes	dark tubes
Number of copulations	15	17	18
Number of palp applications	30	37	91
Maximum applications	2	3	9
Minimum applications	2	2	1
Median applications	2	2	5.5

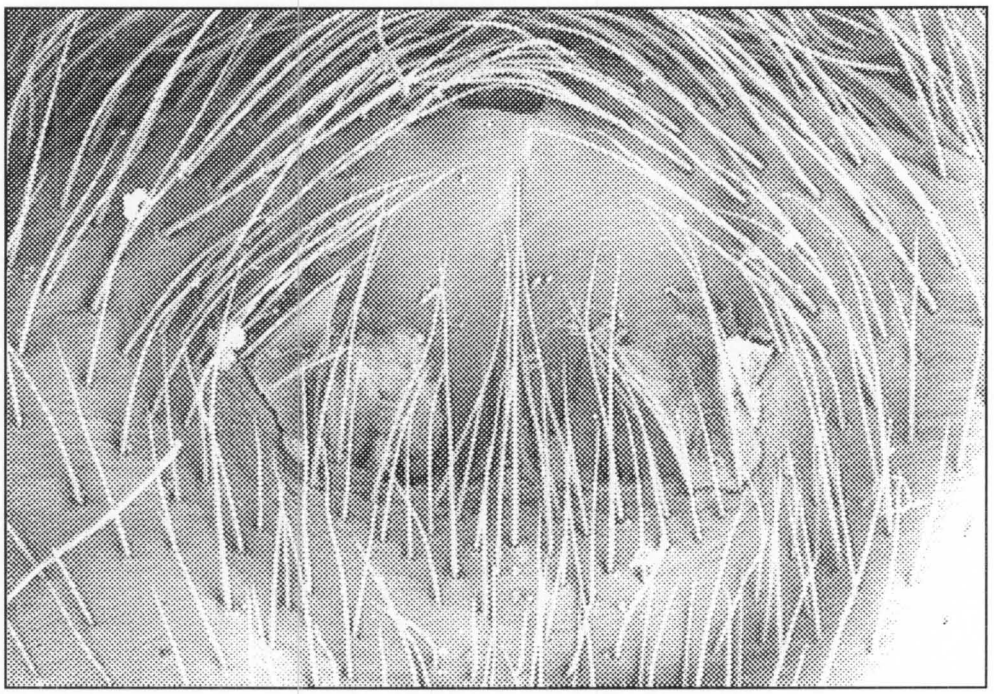
Table 5. Duration of palp applications (minutes) during copulations involving virgin and mated *Trite planiceps* females in light and in dark tubes

	Virgin females		Mated females
	light	dark tubes	dark tubes
Number of copulations	15	17	18
Maximum duration	22.05 min	79.26 min	44.36 min
Minimum duration	58 s	5.27 min	48 s
Median duration	11.53 min	26.49 min	6.28 min

Table 6. Total copulation durations (minutes) for virgin and mated *Trite planiceps* females in light and in dark tubes

	Virgin females		Mated females	
	Light	dark tubes	light	dark tubes
Number of interactions	32	17	32	29
Number of copulations	17	17	0	18
Maximum copulation duration	38	119	-	92
Minimum copulation duration	19	18	-	5
Median copulation duration	23	61	-	39

A



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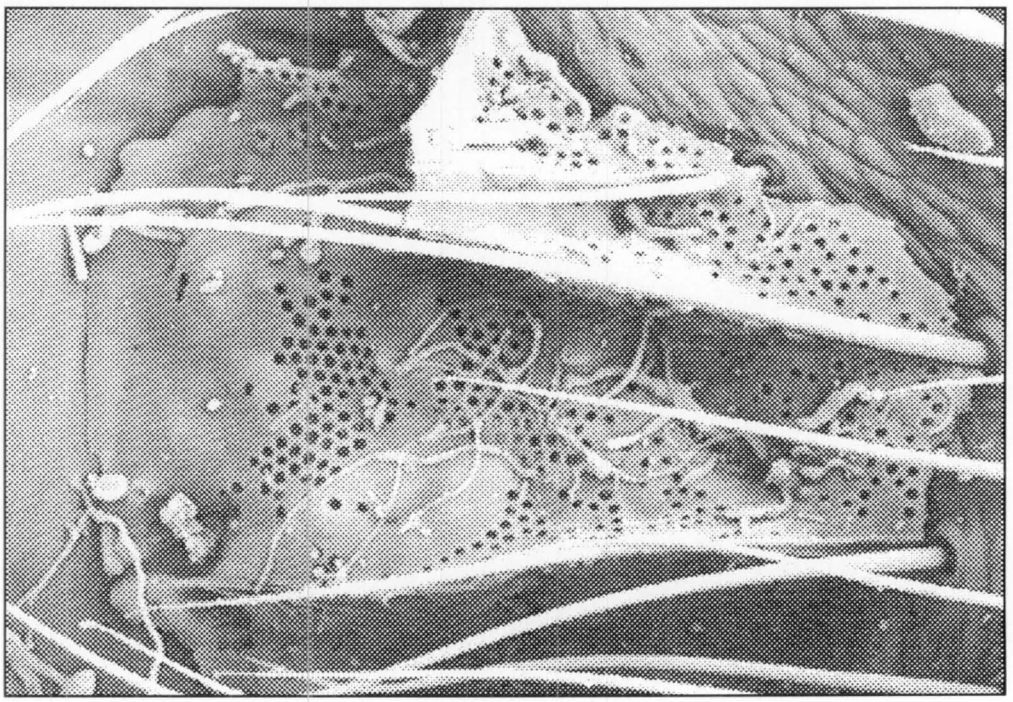


Figure 20. Scanning electron micrographs showing deposits remaining in a *Trite planiceps* female's genital pores following mating. (A) both pores. (B) Closer view of left pore shown in A.

DISCUSSION

The conditional signalling strategies of typical salticids include visual signals when in light away from nests, vibratory signals when communicating at nests, and tactile signals when touching conspecifics (Jackson 1992; Richman & Jackson 1992). *Trite planiceps* possesses all these general salticid traits. Many displays used by *T. planiceps*, especially those used in light, are very similar to displays reported in various other salticid species (Crane 1949; Richman, 1982), and many previously used terms have been retained in the present study. But in addition to possessing all these typical salticid characteristics, *T. planiceps'* display repertoire also includes some very unusual elements that appear to be especially appropriate, and likely adapted, for communicating in its unusual habitat.

Displaying at openings of rolled-up leaves

That *T. planiceps* males display while walking toward openings of rolled-up leaves, even when no conspecific is visible, is a particularly remarkable finding. Because males displayed even when resident females were removed, cues coming directly from females are clearly not essential. The rolled-up leaves used in this study were almost certainly covered by draglines deposited by the resident females, but it is unlikely that cues from draglines alone were responsible for release of these displays; although *T. planiceps* males do preferentially associate with areas containing draglines deposited by conspecific females (Chapter 3), these draglines do not release displays when no rolled-up leaf is present (Jackson 1987). Cues from the leaf itself appear to be necessary for the release of displays in males walking toward the entrances to rolled-up flax leaves. It is not known whether cues from leaves are sufficient when no draglines are present, however.

Although no other spider was visible, it is nonetheless possible that the intended

recievers of apparent signalling by males approaching openings of rolled-up leaves are undetetected conspecifics watching from the dark shadows at the openings. Their dark anterior colouration makes *T. planiceps* at entrances difficult to discern against the dark background of the cavity. In nature and in the laboratory, females were sometimes seen standing just inside the openings to rolled-up leaves or dark tubes. Perhaps males display 'just in case' they are being watched. An alternative explanation is that, despite having the appearance of visual displays, these behaviours actually function as vibratory signals. Leaves are good substrates for transmission of vibrations (Schmitt *et al.* 1994) and it seems very likely that tapping on-erect legs and twitching abdomens would be sufficiently forceful to set up vibrations in the leaves. Similar behaviours have been associated with substrate vibrations, and even audible sounds, in other salticids (Bristowe 1958; Gwynne & Dadour 1985; Maddison & Stratton 1988a,b).

Males of another salticid, *Euryattus* sp., has been reported to also signal when on the outside of rolled-up leaves containing prospective mates. Females of *Euryattus* sp. live inside dry, rolled-up, leaves that they suspend using heavy silk guy-lines (Jackson 1985a). After seeing a suspended leaf, males climb down onto the leaf and then abruptly flex their legs to make the leaf rock to and fro. The female then comes out of the cavity within the leaf and either mates or drives the male away. For both *T. planiceps* and *Euryattus* sp., the unusual habitats occupied by females appears to have favoured the evolution of appropriately unusual signalling behaviour in males.

Signalling in darkness within cavities formed by rolled-up leaves

Many salticids have been reported to rely on silk-bound vibratory signalling when interacting with conspecifics at nests (Jackson 1992). *Trite planiceps* resembles these other salticids; probing, chewing, tugging, up-and-down palpating, abdomen twitching, holding

lunging and forward tapping all probably set up vibrations in nest silk and likely function as signals. But *T. planiceps* is distinguished from all other studied salticids by also apparently signalling by substrate vibrations in darkness when away from nests. When away from nests in darkness, females forward tapped, twitched their abdomens, and holding lunged. Males forward tapped and twitched their abdomens; reciprocal high forward tapping during male-male contests was the most dramatic and apparently ritualised pattern observed. That vibrations were transmitted is strongly suggested by the behaviour of other spiders; when one male forward tapped the substrate, the other male sometimes leaned backwards and raised its Legs I, an apparent defensive posture. Holding lunges are used by females of some other salticids when inside nests signalling to males outside (e.g., Jackson 1989; Jackson & Willey 1995) but living inside rolled-up leaves, an elastic substrate, has apparently allowed *T. planiceps* to adopt a more general use of this behaviour. These interactions were staged in glass tubes, a substrate that would be poor medium for transmission of vibratory signals when compared with the dry leaves where these interactions would take place in nature. If anything, vibratory signalling by *T. planiceps* interacting in the dark cavities formed by rolled up leaves is likely to be even more elaborate and extensive than I have described here.

Vibratory signalling through leaves in light when recievers are out of view

Trite planiceps males tap on-erect legs and twitch their abdomens when females move out of view during interactions in light. Similar apparent vibratory signalling to conspecifics out of view has been reported in males of *Asemonea tenuipes*, which twitch their abdomens while standing on leaf surfaces opposite females, and in addition 'jerk' their bodies just before moving from one leaf surface to the other (Jackson & MacNab 1991). For both *A. tenuipes* and *T. planiceps*, spiders sometimes respond to conspecifics walking on leaf surfaces opposite them,

and so it is very likely that they would readily detect vibrations set up in leaves by twitching abdomens, tapping on-erect legs, and jerking.

The multi-media nature of 'visual' displays

Elaborate visual signalling is probably the most known, and studied, aspect of salticid biology. Recent advances using computer animation techniques confirm that visual signals alone can be sufficient for release of appropriate behaviours in recipients (Clark & Uetz 1992, 1993). But this does not mean that visual signalling is the only communication taking place during 'visual' interactions. Simultaneous with visual signalling, salticids may also be communicating using both air- and substrate-borne pheromones and vibrations (Crane 1949; Gwynne & Dadour 1985; Jackson 1987).

Many visual displays used by salticids involve intense movements of abdomens, whole bodies, legs and palps. These movements appear to be especially well developed in some salticids that live on elastic substrates, indicating a possible concurrent role as vibratory signals. For example, *Epeus* sp. and some lyssomanine salticids, all of which live on broad leaves, have courtship displays that involve up and down jerking of the whole body and abdomen twitching (Jackson 1988; Jackson & MacNab 1991). As well as serving as visual signals, these displays might send vibratory signals through the leaves. Similarly, tapping on-erect legs and abdomen twitching by *T. planiceps* during interactions in light might set also up vibratory signals. The speculation that these visual displays contain vibratory elements is supported by the fact that these same displays are also sometimes used when no conspecific is visible.

Members of the primitive subfamily Spartaeinae vary in characters that suggest a role for physical qualities of interaction sites as a factor directing signal evolution. Most spartaeines invade webs to hunt the host but, unlike many other spartaeines, *Portia* spp. also build webs

themselves and interact with conspecifics in these webs (Jackson & Hallas 1986a,b). Visual displays of web-inhabiting *Portia* spp. cause distinctive movements in the web to which the other spider responds, even when denied visual cues from the other spider (Jackson & Hallas 1986a). In contrast, *Brettus adonis*, *B. cingulatus* and *Cyrba algerina*, spartaeines that invade, but do not live in, webs, appear to make little or no use of vibratory signalling during intraspecific interactions (Jackson & Hallas 1986b). Physical qualities of interaction sites (substrate elasticity) appears to determine the extent of vibratory signalling in spartaeine salticids.

The relationship between habitat, resting posture and nest stucture

In addition to signalling behaviour, habitat may also influence other aspects of *T. planiceps'* life. *Trite planiceps'* unusual resting posture seems to be especially appropriate in its unusual habitat. Using its 'linear' resting stance, with the legs extended in line with the body, *T. planiceps* can fit into crevices that would exclude similar-sized salticids that adopt more typical resting postures.

Trite planiceps' nest is also unusual, and likely to be adapted to life inside rolled-up leaves. Typical salticid nests are more or less tubular cocoons that completely enclose the resident (Hallas & Jackson 1986a). Some species additionally build a sparse, flat, roof over the nest. Although *T. planiceps* females sometimes built a roof over the nest, extending down from the opposite side of the rolled-up leaf, they were never seen in fully enclosing nests. Amongst other functions, spider nests regulate humidity around the eggs and protect the resident and her offspring from free water (Hieber 1984). Perhaps building the nest at a well-sheltered site that provides protection from free water and fluctuations in humidity makes an enclosing cocoon un-necessary for *T. planiceps*.

Interestingly, *Marpissa rumpfi*, a European salticid that is only distantly related to *T. planiceps*, lives in hollow reeds that physically resemble the rolled-up flax leaves occupied by *T. planiceps*. *Marpissa rumphi* builds an unenclosed nest that is remarkably similar to that of *T. planiceps* (Holm 1940). Such apparent convergence in nest structure of distant relatives suggests that this nest structure has evolved more than once and may be parallel adaptation for life in rolled-up leaves.

Sex and site differences in receptivity and copulation

Trite planiceps males were apparently always receptive, invariably courting females that they encountered in light or in dark tubes. In contrast, females varied in receptivity depending on whether they were in light or in dark tubes, whether a nest was present, and whether they were virgin or mated. Relatively greater receptivity in males and similar differences in receptivity of females depending on interaction site, sex, and mating history have been reported in other salticids (Jackson 1978a,c; Jackson & Harding 1982), and appear to be a common feature of salticids.

The greater receptivity of mated females in dark tube when compared with in light, may be explained by relative exposure to predators. *Trite planiceps* shares its habitat with diurnal predators, including birds, pompilid wasps, lizards, and spiders (pers. obs.). Spiders would be at risk from these predators when mating in the open, but would be protected when mating inside rolled-up leaves. But why should this predation risk be more relevant to non-virgin than virgin females? There are two likely reasons. First, copulation may be more valuable for virgin than for mated females, because virgins need sperm to reproduce. This additional benefit for virgins might be sufficient to counter costs of predation risk. Second, virgin females may be more likely to recieve sperm when mating than are mated females, because copulation may be

hindered by mating plugs deposited by previous mates (Jackson 1980a; Austad 1984). Substances seen in the genital pores after mating may have been mating plugs, and that mated females have difficulty re-mating is suggested by more variable frequency and rate of palp applications when mating inside dark tubes (Tables 3, 4, 5). These factors may all combine to make copulations in light 'uneconomic' for mated females.

Predictors of contests outcome, and sex differences in agonistic behaviour

For *T. planiceps*, relative size was a good predictor of outcome for all types of contests in light; larger spiders tended to beat smaller rivals. A tendency for relative size to predict contest outcome has been reported previously for juveniles of *T. planiceps* (Forster 1982c), and for adults of other salticids (Wells 1988; Jackson & Cooper 1991; Faber & Baylis 1993). But outcome was not the only role for relative size in the interactions of *T. planiceps*. For some types of interactions smaller spiders tended to see larger spiders first and juveniles and subadult females that saw adults appeared to make use of this opportunity to avoid detection by remaining still or decamping. Adult females, however, were especially prone to using this opportunity to stalk and then leap at conspecifics. Females of another New Zealand salticid, *Marpissa marina*, also commonly make use of this opportunity to stalk and leap, rather than display at, rivals (Jackson *et al.* 1990) and, like *T. planiceps*, these *M. marina* females sometimes catch and kill the other spider.

There are species and sex differences both in tendency of salticids to interact with conspecifics and in the ways that spectators incite interactions (Jackson & MacNab 1989a,b; Jackson *et al.* 1990). Decisions about whether and how to avoid or incite interactions are surely commonplace in the lives of salticids but the importance of decisions made prior to, and sometimes precluding, interactions has rarely been considered.

The outcome of contests between *T. planiceps* males within dark tubes was predicted by both relative size and residency but effects of residency appeared to over-ride the effects of relative size in contests between females. The resident-intruder asymmetry in contests between *T. planiceps* females may result from an asymmetry in costs of losing rather than in benefits of winning or in intrinsic fighting ability. To lose, an intruder can simply retreat away from the resident and safely depart but, to lose, a resident must move past the intruder. Females often lunged and grabbed at each other, and in one case grasping and killing the other spider, so it is dangerous for a small resident to move past a larger intruder. Residents seem to be quite immune from attack when they retreat into the restricted area, and can simply wait out the seige there until the intruder gives up and decamps. That is, the residence asymmetry in female-female contests likely arises from an extrinsic component of fighting ability (Parker & Rubenstein 1981). A resident-intruder asymmetry has been reported during contests between female *M. marina* at nests (Jackson & Cooper 1991), and a similar logic may underly the asymmetry in these contests. This asymmetry may be less apparent during male-male contests because males rarely lunge and grab or attempt to bite rivals; a smaller resident can quite safely walk past a larger intruder and decamp from the dark tube.

Overall, females tended to behave more aggressively than males in all situations. When interacting in light, females stalked and often leaped at other females, subadult females, juveniles, and sometimes at males. In contrast, males never stalked or leaped at females, subadult females or juveniles, and only rarely stalked or leaped at other males. When interacting in dark tubes, females often lunged and grabbed at males or other females, in some cases catching the other spider. Males, on the other hand, only rarely lunged at rivals or prospective mates and never injured or killed other spiders during interactions. Additionally, the display repertoires of males contained more elements and appeared to be more highly

stereotyped. This trend has also been reported in many other salticids (e.g., Jackson & Hallas 1986a,b; Jackson & MacNab 1989b; Jackson *et al.* 1990) and in spiders from other families (Fernandez-Montraveta & Ortega 1993). The reasons underlying these, and other, trends in the display behaviour of salticids will only become apparent once a more expansive comparative data base and more intensive species studies of signal function are available.

CHAPTER 3

Pheromonal and visual cues used by *Trite planiceps* Simon (Araneae, Salticidae) during mate-location

ABSTRACT

Trite planiceps (Salticidae) lives in the cavities formed by rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants. This study presents evidence that *T. planiceps* males use cues from female's draglines deposited on the outside of these rolled-up leaves when searching for females hidden from view inside. When given the options of being on areas containing fresh draglines of conspecific females and areas containing no draglines, *T. planiceps* males preferentially associated with the draglined areas. Females did not discriminate between areas with and without male's draglines and neither males nor females discriminated between areas with and without same-sex conspecific's draglines. When tested in an arena containing a rolled-up leaf that had been occupied by a female in nature, males found and entered the cavities within rolled-up leaves sooner when leaves had been collected within 24 hours (draglines deposited on leaves in nature) than after the same leaves were cleaned and aged for 7 days (dragline cues removed). Shorter latency to finding of leaf openings was restored after the same leaves were subsequently occupied by females in the laboratory (dragline cues replaced). This is the most direct evidence to date that cues from female's draglines are present and used by male salticids searching for mates in nature. The specific relevent cues are probably pheromones loosely bound to female's draglines.

Trite planiceps males displayed at openings of rolled-up leaves, even after dragline cues

had been removed. This is an unusual instance of display behaviour being released in males by a habitat feature that is sometimes associated with conspecific females in the apparent absence of any cues coming directly from conspecific females. This behaviour is likely a special adaptation to *T. planiceps'* unusual habitat.

INTRODUCTION

Jumping spiders (Salticidae) are distinguished from other spiders by having complex eyes and remarkably acute vision (Blest *et al.* 1990), and are well-known for their elaborate use of vision when hunting, navigating, and communicating (Crane 1949; Hill, 1979; Forster 1982a Clark & Uetz 1993). Yet recent evidence suggests that cues associated with female's draglines are especially important to male salticids searching for mates. Males of *Carrhotus xanthogramma* both walk more slowly and recognise dummy females as prospective mates more frequently when female's draglines are present (Yoshida & Suzuki 1981) and males of *Portia fimbriata*, *P. labiata* and *Phidippus audax* preferentially associate with areas containing draglines recently deposited by conspecific females (Oden 1981 in Pollard 1987; Clark & Jackson in press a).

Females of *Trite planiceps*, a common New Zealand salticid, build their nests in the cavities formed by the rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants (Forster & Forster 1973; Chapter 2). There is usually only a single small opening to these cavities (Fig. 1); males seeking females hidden from view inside rolled-up leaves face the challenge of finding these openings in a habitat containing many similar leaves that do not contain females. Cues associated with draglines left by females walking about on their 'home leaves' may allow males to discern leaves occupied by potential mates and hence target their mate-searching effort toward leaves offering higher returns. After contacting female's draglines

on leaves, *T. planiceps* males display at the entrances to rolled-up flax leaves, and enter rolled-up flax leaves that contain conspecific females on nests (Chapter 2). However, the relative importance of visual cues and pheromones for this response to the entrances to rolled-up leaves in unknown. In this chapter I investigate how *T. planiceps* males use dragline and visual cues when seeking mates.

METHODS

Trite planiceps males and females were collected near Christchurch, New Zealand 2-4 weeks prior to testing and were maintained using standard methods (Jackson & Hallas 1986a). Unless specified otherwise, all statistical comparisons are by Wilcoxon signed-ranks tests.

Tests of substrate preferences

This experiment was designed to investigate the tendencies of *T. planiceps* males and females to associate with or avoid areas containing draglines deposited by same-sex and other-sex conspecifics. The arena was a constructed from a 90 mm-diameter plastic petri dish (Fig. 2). The petri dish (base and lid) was cut in half, and an opaque plastic screen was glued into each half-base midway between the cut edge and the point of greatest distance to the cut edge (see Clark [1993] for rationale of arena design). A 10 mm-diameter half-circle hole was melted into the cut edge of each half petri dish immediately adjacent to the wall at the end to which the screen was fixed.

One 'half-arena' was selected at random to be 'draglined'. The half-circle hole and open side of this half-arena was taped over and a 'source-spider' was introduced. The source-spider was left for 2 h to deposit draglines and, after removing the source-spider, the draglined half-arena was used in a test within the following 2 h.

To begin a test, the draglined half-arena was matched up with a clean half-arena so that the half-circle holes on the edge of the half-arenas formed a single 10 mm-diameter hole in the floor. The test spider was placed in a clear plastic 'transfer tube' (40 mm long, 10 mm external diameter) which was then corked at both ends. The transfer tube was inserted into the hole in the arena floor so that the tube protruded 1-2 mm into the arena and was held in place by the two half-arenas pressing together. The cork protruding into the arena was then removed. The 'test-spider' climbed up out of the transfer tube into the arena, and the test began when the spider's palps were above the arena surface. The amount of time that the test spider spent on each side of the arena was recorded for 10 min, using the palps as the point of reference for location. If a spider stood with one palp on each side of the arena, it was counted as still being on the side previously occupied by both palps (i.e., failing to move to the other side). Each spider was only used once as a test spider or source-spider.

Mate searching on rolled-up leaves

This experiment was designed to investigate whether mate-searching by *T. planiceps* males is facilitated by draglines left by conspecific females on leaf surfaces in the laboratory, and whether similar cues are present on leaves in nature. Twenty rolled-up flax leaves containing *T. planiceps* nests and maternal females were collected on the evening prior to testing ('fresh' leaves). Fresh leaves would typically be covered by draglines deposited by resident females in nature. Residents were removed, and the rolled-up leaves were cut to 500-550 mm long with the opening near the middle.

On the day of testing, each rolled-up leaf was mounted on a tripod with two other dried leaves (500-550 mm long) that were not rolled-up (Fig. 3). The tripod and leaves were placed in a glass tank (300 mm x 300 mm floor, 600 mm high). The opened cage of a *T. planiceps*

male was placed on the tank floor and the tank was closed with a glass lid. All experiments were started in the middle 2 h of the laboratory light phase (12L:12D). Each tank was checked at 5-min intervals for a maximum period of 5 h after the male left his cage; at each check whether the male had entered the cavity within the rolled-up leaf was recorded. If the male could not be seen, the rolled-up leaf was carefully un-rolled to confirm that the male was inside (end of test).

After tests ended, the glass tanks, tripods and leaves were thoroughly washed with distilled water and then ethanol to remove draglines and pheromones. They were then left for 7 days, so that any remaining pheromones could dissipate, and the testing procedure was repeated. This treatment was called 'cleaned leaves', which was justified because, in other salticids, aging and washing are known to eliminate the effectiveness of draglines at eliciting associative behaviour and courtship of males (Jackson 1987; Clark & Jackson in press a).

After tests using cleaned leaves, the tanks, tripods and leaves were washed again and allowed to dry for 24 h. The adult female that was in the leaf in nature was then replaced in the leaf, left for 7 days, and testing was repeated again ('lab-draglined leaves'). On the day before testing a lab-draglined leaf, the resident was removed and the whole arena (tank, tripod, leaves), except the rolled-up leaf, was washed.

The same group of males was used for the tests using fresh, cleaned, and lab-draglined leaves, but each male was used only once in tests of each type and the same male was not used for more than one test of a particular leaf. To ensure that results were not confounded by shrinkage of the openings of rolled-up leaves during the interval between tests, the maximum width and length of openings were measured to the nearest millimetre following the first and third tests, and compared.

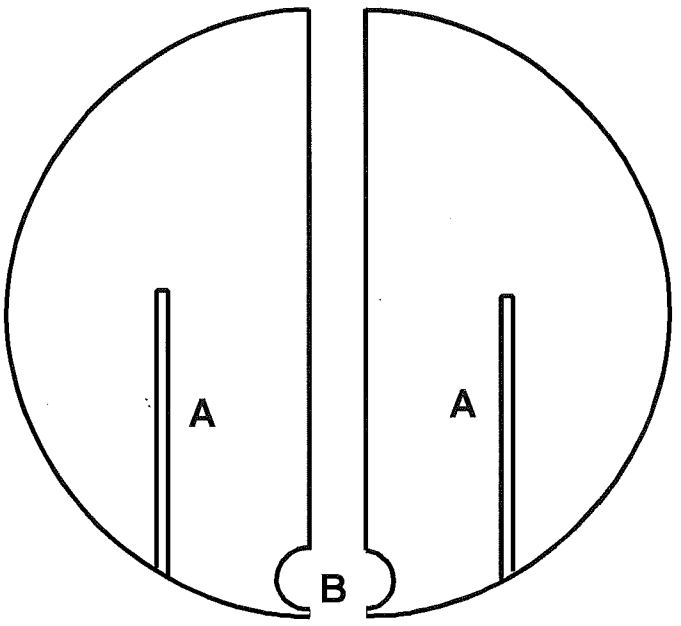


Figure 1. Diagram of testing arena used to investigate substrate preferences. (A) Opaque plastic screens. (B) Hole for insertion of the tranfer tube (when the two halves are pressed together).

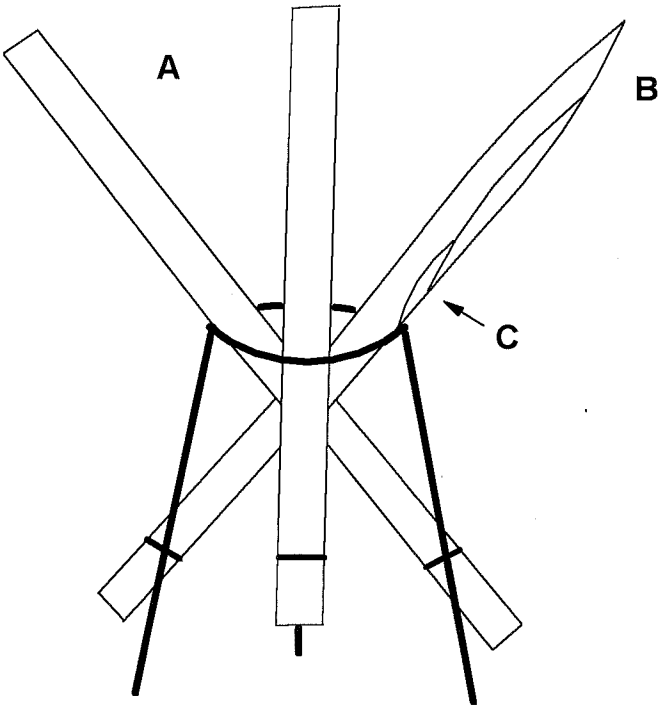


Figure 2. Diagram of testing arena used to investigate effects of dragline cues on mate-searching efficiency. (A) Two dry leaves that are not rolled up. (B) Dry, rolled-up leaf. (C) Entrance to the cavity within the rolled-up leaf.

RESULTS

Substrate preferences

Males spent more time on the side of the arena containing draglines of conspecific females than on the clean side but there was no evidence that females (mated or virgin) associated with or avoided draglines deposited by males (Table 1). Also, neither males nor females showed any tendency to associate with or avoid draglines of same-sex conspecifics (Table 1).

Mate-searching efficiency on rolled-up leaves

Males found the openings and entered the cavities within rolled-up leaves during the 5 h testing period in all tests using fresh or lab-draglined leaves, and in 18 of 20 tests using cleaned leaves (X^2=4.14, $df = 2$, $P > 0.1$). However, latency until entering cleaned rolled-up leaves (median 83 min; range 5-300 min) was greater than for fresh leaves (median 23 min; range 5-210 min; $P < 0.01$) or lab-draglined leaves (median 16 min; range 5-190 min; $P < 0.005$). There was no evidence that latency to entry of rolled-up leaves differed for fresh and lab-draglined leaves ($P > 0.2$). Also, there was no evidence that length or width of the openings to rolled-up leaves changed during the 3-week interval between tests (for both, $P > 0.9$).

Behaviour during mate-searching

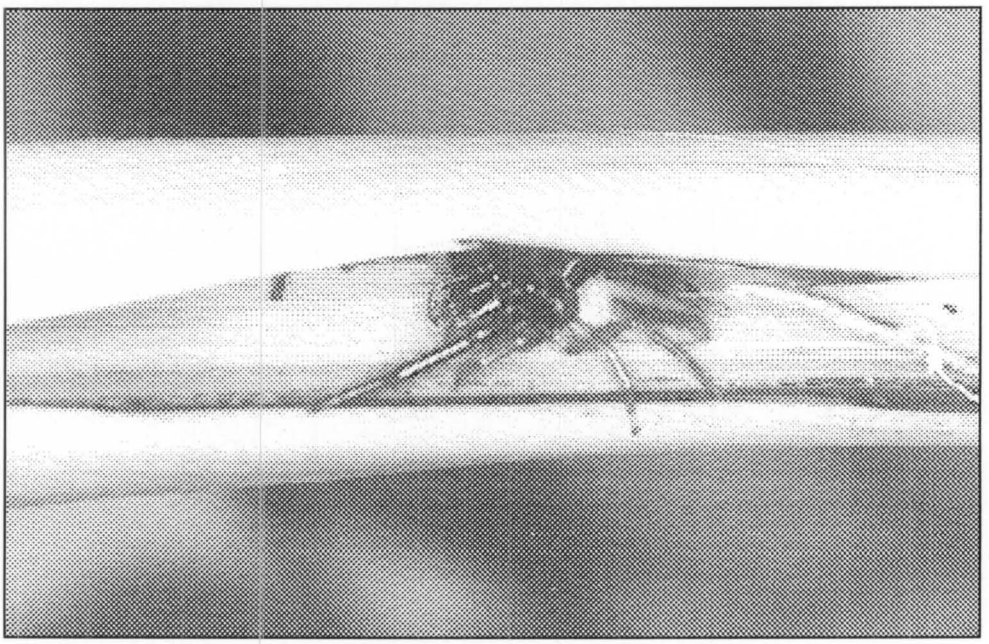
When on fresh or lab-draglined leaves, but out of sight of entrances, males walked frequently and rapidly in short bursts lasting 0.1-0.5 s broken by pauses of 1-15 s. Males palpated the leaf surface whenever they stopped, and sometimes twitched their abdomens while walking up the leaf. Males on cleaned leaves walked more continuously and rarely palpated or twitched their abdomens.

After seeing openings of rolled-up leaves, however, the behaviour of males on cleaned leaves could not be distinguished from the behaviour of males on fresh leaves or lab-draglined leaves. Males on-erect postured, tapped on-erect legs and twitched their abdomens while approaching the openings. When males reached the leaf openings, they usually leaned forward into the cavities and high forward tapped. Males then walked into the cavity within the rolled-up leaves. Males frequently high forward tapped and twitched their abdomens as they entered rolled-up leaves (Figs. 2 & 3), and usually turned through 180° several times just inside the entrance so that they high forward tapped while facing both directions along the leaf interior.

Table 1. Proportions of total time spent on the draglined half-arena *vs.* clean half-arena.

	N	median	Upper quartile	Lower quartile	*P*
Males on female's draglines	23	0.79	0.91	0.54	<0.01
Mated females on male's draglines	29	0.48	0.77	0.30	>0.9
Virgin females on male's draglines	37	0.47	0.63	0.34	>0.2
Males on male's draglines	36	0.50	0.68	0.36	>0.9
Females on female's draglines	40	0.59	0.69	0.41	>0.1

A



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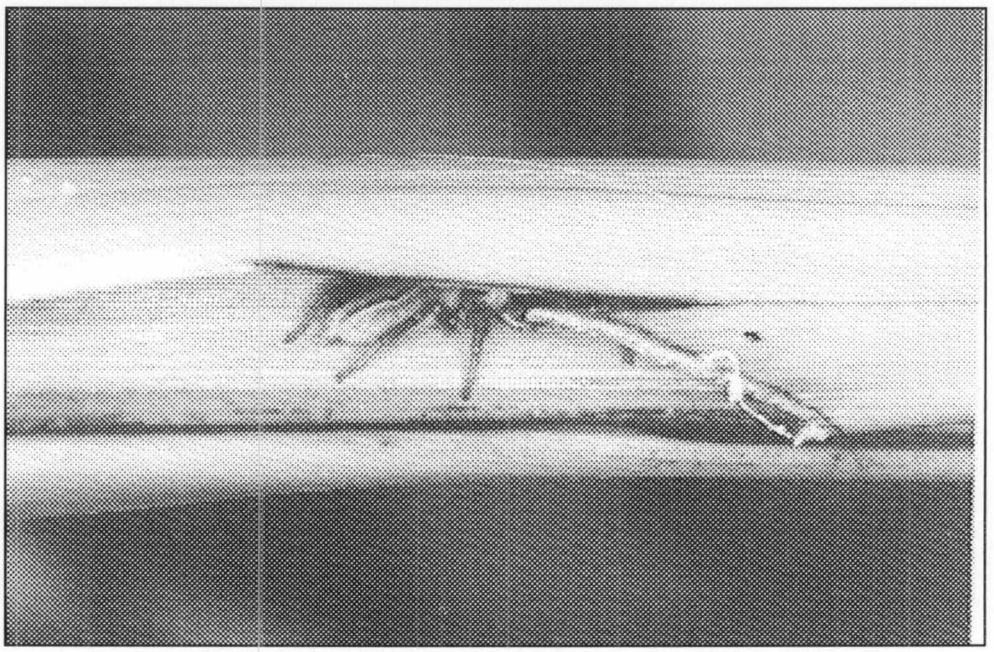


Figure 3. *Trite planiceps* male high forward tapping while facing in both directions when entering the cavity within a rolled-up flax leaf.

DISCUSSION

Males of many salticids, including *Trite planiceps* have been reported to recognise nests of conspecific females by using polar pheromones associated with the silk (Jackson 1987). These spiders begin courting when on unaltered nests, but fail to court after nests have been aged or immersed in polar solvents. Males of some, mostly primitive, salticids also begin courting when on female's draglines. Although female's draglines do not elicit courtship in *T.planiceps* males (Jackson 1987), the present study shows that female's draglines do elicit associative behaviour. In this respect, *T. planiceps* resembles *Portia fimbriata* and *P. labiata* (Jackson 1987; Clark & Jackson in press a).

The specific relevant cues eliciting association in *T. planiceps* males are probably pheromones loosely bound to the silk of females (Jackson 1987). For both *Portia* spp. studied by Clark & Jackson (in press a), associative behaviour was not detected if the draglines were left for 7 days prior to testing and for *Phidippus audax* associative behaviour could be prevented by immersing the female's draglines in certain solvents (Oden 1981 in Pollard *et al.* 1987). These findings indicate that associative behaviour is elicited by pheromones rather than physical properties of female's draglines. It is also likely that association with draglines and courtship on nests is elicited by the same pheromone. In *Phidippus johnsoni*, males court on nests but not draglines, but court on amassed draglines as though they were nests (Jackson 1987). That is, the difference in male responses toward female's draglines and nests appears to depend on substrate texture, a physical quality, rather than chemistry.

In addition to associating with female's draglines in choice tests, *T. planiceps* males also found female's nesting sites sooner when female's draglines were present on rolled-up leaves. It could be that males found the female's nesting sites sooner simply because they remained in the vicinity for longer when draglines were present. However, it is also possible that female's

draglines induce more specific changes. Female salticids, especially those of semelparous species, typically reside at a single nest with their developing young for many weeks (Jackson 1978b; Chapter 5). These females presumably forage nearby, coming and going repeatedly. Consequently, a male that finds itself on an area containing accumulations of female's draglines of the densities used in salticid studies is probably very near to the female's nest. Males on female's draglines do not simply sit still and wait for a female to appear; they walk about, repeatedly palpating the substrate, apparently searching. Perhaps these males are searching both for prospective mates directly (Yoshida & Suzuki 1981) and also for certain sites, such as the openings of rolled-up leaves, that are likely to be occupied by prospective mates. Females of many salticids build nests and attend eggs in a very limited range of characteristic sites (Mikulska 1961; Jackson & Harding 1982; Jackson & McNab 1991), and males may search for these sites. Use of topographical cues to direct searching when direct cues from resources are unavailable is commonplace amongst a wide range of parasitoids, predators, and herbivores (Bell 1991).

The present study of *T. planiceps* has one important feature lacking in all previous studies using other salticids. In addition to using draglines deposited in the laboratory (all tests of association and 'lab-draglined' leaves), I also used substrates on which draglines were deposited in nature ('fresh' leaves). Identifying a similar response to lab-draglined and fresh leaves strengthens the assertion that dragline cues are present and used by *T. planiceps* males searching for mates in nature.

The importance of pheromonal and visual cues for release of displays

Pheromonal cues associated with female's draglines do not appear to be essential for *T. planiceps* males on rolled-up flax leaves to find openings, display at these openings, and

finally enter cavities within the rolled-up leaves. This appears to be the first report of intraspecific display behaviour being released in a salticid solely by physical stuctures that are commonly associated with females when no direct cues from females are present. *Trite planiceps* males appear to have evolved an ability to visually recognize a habitat feature that is commonly associated with conspecific females.

CHAPTER 4

A case of blind spider's buff?: Prey-capture by jumping spiders (Araneae, Salticidae) in the absence of visual cues

ABSTRACT

Jumping spiders (Salticidae) are well-known for remarkably adapted visual hunting, but this is the first study to assess whether salticids also commonly possess the ability to catch prey in the absence of visual cues. When tested inside tubes, where spiders and prey (house flies, *Musca domestica* L. and fruit flies, *Drosophila* spp.) could not easily evade each other, each of 42 species of salticid tested caught prey in the absence of visual cues in at least one of four different procedures used. Some salticids caught flies less frequently or were less aggressive when tested in petri dishes, where spiders and flies could easily evade each other. For both types of arena and prey, there were significant interspecific differences in both success at prey-capture and tendency to act aggressively when first contacted by flies. Additionally, there was significant positive correlation between success at catching prey and tendency to act aggressively when first contacted. Salticids resembled short-sighted spiders from other families by not attempting to catch flies before physically contacted, and by lunging to catch prey (when visual cues are available, most salticids usually leap on prey). Why salticids differed in capture success and aggressiveness in these tests and circumstances in nature when salticids might use their ability to catch prey in the absence of visual cues are discussed.

INTRODUCTION

Jumping spiders (Salticidae) have visual acuity that far exceeds the abilities of other spiders (Land 1985; Blest *et al.* 1990). Acute vision in salticids is provided by highly developed antero-median (principal) eyes that are structurally unlike the eyes of other spiders (Williams & McIntyre 1980). The salticid's other (secondary) eyes are relatively unmodified, and function as movement detectors providing coverage of almost 360° around the spider (Forster 1979; Land 1985). After detecting moving objects with the secondary eyes, the salticid executes a precise turn to orient the principal eyes toward the stimulus (Land 1971). Using the principal eyes, the salticid then accurately identifies the stimulus source from distances of up to 30 body lengths (Jackson & Blest 1982a).

Salticids are well known for their use of acute vision when communicating (Crane 1949; Clark & Uetz 1994), navigating (Hill 1979; Tarsitano & Jackson 1992) and hunting (Forster 1977a). Although members of some other spider families may make limited use of vision when hunting (e.g., Snelling 1983; Stratton 1984; Jackson *et al.* 1995), no non-salticid comes close to the refinement of vision-mediated hunting behaviour used routinely by salticids. Once oriented toward a target, a salticid uses visual cues when making decisions not only about whether but also about how the hunt should proceed. For example, visual cues about prey size, distance and orientation influence the salticid's speed and direction of approach (Freed 1984; Jackson & van Olphen 1991). If a direct path to the prey is not possible, the salticid uses its vision to plan a detour that brings it closer to the prey by an indirect path (Jackson & Wilcox 1993a; Tarsitano & Jackson 1992). The salticid slowly creeps up on its prey until close enough for an attack, pauses, and then finally leaps at the prey (Heil 1936; Drees 1952; Forster 1977a).

Although their use of vision when hunting has been extensively studied, whether salticids can also catch prey when denied visual cues has rarely been considered and laboratory

studies have given conflicting evidence. When tested in large arenas, *Phidippus johnsoni* failed to catch prey in the absence of visual cues (Jackson 1977a), but *Trite planiceps* was later found to catch prey when tested in smaller arenas (Forster 1982b). Evaluation of whether *T. planiceps* is unusual in its ability to catch prey in the absence of visual cues requires comparative data from a broad array of salticid species from this large and diverse spider family (see Coddington & Levi 1991).

In the present chapter, I investigate the non-visual prey-catching abilities of salticids from 17 subfamilies, including species with diverse 'lifestyles' (e.g., foliage-dwellers, ground-dwellers, active hunters, ambush hunters, web-invading araneophages, web-builders, ant-mimics, myrmecophages) and widely different geographic regions (Table 1). For comparative purposes, I also investigate the non-visual prey-catching abilities of some non-salticid hunting spiders (i.e., spiders with comparatively poor eyesight) from the same habitat as *T. planiceps*.

Because salticid eyes are not sensitive to infra-red light (Blest *et al.* 1981; Yamashita 1985; Peaslee & Wilson 1989), infra-red video was used to observe the behaviour of spiders in the absence of visual cues. This is amongst the first studies to make use of this technology to study the behaviour of salticids (see also Taylor 1995).

MATERIALS AND METHODS

Spiders from laboratory cultures were used, excluding individuals that were missing appendages. Cage design and maintenance procedures were as in earlier spider studies (Jackson & Hallas 1986a). Except during experiments, spiders had *ad libitum* access to adult house flies (*Musca domestica* L.) or adult fruit flies (*Drosophila melanogaster* Meigen) as prey, depending on the spider's size. *Portia* spp., for which other spiders are preferred food, had their diets supplemented with various species of spiders, and *Corythalia canosa*, *Natta rufopictus* and

Table 1. Spiders (all salticids except the last 5) tested for ability to catch prey in the absence of visual cues

	Subfamily[1] (Family[2])	Origin	adult body length (mm)
Asemonea tenuipes	Lyssomaninae	Sri Lanka	4
Bavia aericeps	Thiodininae	Australia (Queensland)	12
Corythalia canosa	Plexippinae	USA (Florida)	6
Cosmophasis micarioides	Heliophaninae	Australia (Queensland)	7
Cosmophasis bitaeniata	Heliophaninae	Australia (Queensland)	6
Cosmophasis sp.	Heliophaninae	Philippines	7
Cyrba ocellata	Spartaeinae	Sri Lanka	5
Epeus sp.1	Hyllinae	Singapore	8
Epeus sp.2	Hyllinae	Philippines	8
Eris marginata	Dendryphantinae	USA	6
Euophrys parvula	Euophrynae	New Zealand	6
Euryattus sp.	Cytaeinae	Australia (Queensland)	8
Hasarius adansoni	Hasariinae	Australia (Queensland)	6
Helpis minitabunda	Astianae	New Zealand	7
Hentzia mitrata	Dendryphantinae	USA (North Carolina)	5
Holoplatys planissima	Marpissinae	New Zealand	8
Holoplatys sp.	Marpissinae	New Zealand	5
Jacksonoides queenslandica	Astianae	Australia (Queensland)	7
Lyssomanes viridis	Lyssomaninae	USA (Florida)	6
Marpissa marina	Marpissinae	New Zealand	8
Menemerus bivattatus	Marpissinae	Australia (Queensland)	5
Mogrus dumicola	Dendryphantinae	Israel	8
Mopsus mormon	Thyeninae	Australia (Queensland)	12
Myrmarachne lupata	Myrmarachninae	Australia (Queensland)	5
Natta rufopictus	Heliophaninae	Kenya	5
Phidippus johnsoni	Dendryphantinae	USA (California)	9
Phidippus sp.1	Dendryphantinae	USA (Arizona)	9
Phidippus sp.2	Dendryphantinae	USA (Texas)	9
Plexippus calcarata	Plexippinae	Australia (Queensland)	10
Portia africana	Spartaeinae	Kenya	8
Portia fimbriata	Spartaeinae	Australia (Queensland)	8
Portia labiata	Spartaeinae	Sri Lanka and Philippines	8
Portia shultzi	Spartaeinae	Kenya	7
Simaetha paetula	Simaetheae	Australia (Queensland)	8
Tauala lepidus	Astianae	Australia (Queensland)	7
Thiania bhanoensis	Itatinae	Singapore	5
Thorellia ensifera	Spilarginae	Singapore	5
Trite auricoma	Cytaeinae	New Zealand	9
Trite planiceps	Cytaeinae	New Zealand	10
Tularosa plumosa	Hasariinae	Kenya	5
Viciria praemandibularis	Hyllinae	Singapore	10
Zendora orbiculata	Euophrynae	Australia (Queensland)	4
Cheiracanthium stratioticum	Clubionidae	New Zealand	8
Clubiona cambridgei	Clubionidae	New Zealand	8
Dysdera crocata	Dysderidae	New Zealand	10
Supunna picta	Clubionidae	New Zealand	8
Taieria erebus	Gnaphosidae	New Zealand	7

[1] Salticids, [2] Non-salticids

Zendora orbiculata, each of which prefers ants, had their diets supplemented with various species of ants.

Five different testing procedures were used, but all had the six following elements in common: 1) All tests were carried out during the laboratory light phase (12L:12D), excluding the first and last 2 h. 2) Between tests, arenas were thoroughly washed with water and then ethanol to remove silk and chemical cues that may have accumulated during previous tests. 3) Prior to testing, spiders were kept without food for 6-8 days. 4) Spiders were tested no more than once per day. 5) Individual spiders were tested in the dark using only types of prey that they had been observed catching in the light. 6) Spiders were used only once with each prey type in any type of test.

Blinded spiders in horizontal tubes (type 1 tests)

Two days after feeding and six days prior to testing, all eyes of the test spider were coated with two or three layers of opaque enamel paint while the spider was subdued under CO_2. A spider and an adult fly (*M. domestica* or vestigial-winged *D. melanogaster*) were placed at opposite ends of a 120-mm long plastic tube plugged by a cork at each end. The spider and fly were separated by a partition placed in a slit at the mid-point of the tube. Spiders and flies were then left for a 5-min settling-down period before tests were started. To start a test, the partition was removed so that spiders and flies could move around the entire arena. Spiders were observed for 15 min or until predation occurred.

Spiders 6.0 mm or less in body length were tested in 6.4-mm diameter tubes, whereas spiders 6-8 mm in body length were tested in 7.9-mm diameter tubes. Adult females were used for tests of species in which adult body length was 8 mm or less. Juveniles 6-8 mm in body length were used for species in which adult body length was greater than 8 mm.

Blinded spiders in vertical tubes (type 2 tests)

Type 2 tests were used primarily for species that failed to catch flies during type 1 tests. These tests were the same as type 1 tests, except that tubes were oriented vertically instead of horizontally. Spiders were placed in the uppermost half of the tube. Because flies tend to move upwards when given the opportunity, this procedure was adopted as a means of promoting more frequent contact between spiders and flies than type 1 tests.

Sighted spiders in tubes under infra-red light (type 3 tests)

Type 3 tests were the same as type 1 tests except that the arena was made of glass rather than plastic and, instead of blinding the spiders, they were observed using an infra-red (IR) video system. Tests were staged inside a light-proof cabinet illuminated by an infra-red light source and were observed using a video-camera that was sensitive to IR light. The IR video camera was connected to a monitor positioned outside the cabinet so that behaviour of spiders could be observed. The light-proof cabinet had sleeves consisting of a double layer of heavy black satin so that the experimenter could reach in to remove the partition (i.e., begin tests) without allowing light to enter.

Rather than varying the tube diameter with spider size, only adult spiders were used and all spiders were tested in tubes that were 100 mm in length and 11 mm in internal diameter. Fruit flies used were fully winged *Drosophila immigrans* Sturtevant instead of vestigial winged *D. melanogaster*. *Drosophila immigrans* is larger and more active in darkness than is *D. melanogaster*, and the spiders and flies contacted each other more frequently when this species was used in preliminary tests. Instead of adjusting prey size to spider size, all spiders were tested using a 'standard fruit fly' 2.5-3 mm in body length or a 'standard house fly' 7-8 mm in body length. After placing a fly and a spider at opposite ends of the tube with the partition in

place, the tube was placed horizontally in the light proof cabinet. The partition was removed in IR light after the spiders had been in IR light for a 5-min settling-down period. Tests lasted 15 min or until the spiders caught the flies.

In preliminary tests, individual spiders responded to contact with the flies in one of several different ways. A spider might respond in an apparently aggressive manner; it might actually lunge at the fly, or it might carry out apparent preliminaries to lunges, such as orienting toward the fly or raising its front legs. These responses were collectively termed 'confront'. Alternatively, a spider might respond in an apparently less aggressive manner; it might run, walk, or jump away from the fly, turn away from the fly without stepping, or lean away from the fly by flexing legs on the side opposite to the fly. These responses were collectively termed 'avoid'.

Whether spiders and flies physically contacted each other during the 15-min testing period was recorded and responses of spiders to first contact with the fly during tests were recorded as either confront or avoid, the relative proportions providing a general measure of 'aggressiveness' of each species under testing conditions.

If flies were grasped and then released, or if they broke free from spiders during tests, these spiders and flies were kept in IR light for a further 60 min after the 15-min testing period ended. This enabled me to investigate whether the flies died and, if the flies died, whether the spiders later picked up the dead flies and ate them. When flies died after being bitten, this was recorded as a capture.

Sighted spiders in petri-dishes under infra-red light (type 4 tests)

The arena used in type 4 tests was a plastic petri dish (85-mm in diameter) with a plastic tube (30 mm long, 7 mm internal diameter) glued onto a hole in the wall. A standard house fly

(i.e., 7-8 mm body length) was placed into the tube. A partition inserted into a slit at the petri dish-end of the tube and a wooden plunger inserted into the other end of the tube prevented the fly's escape. Next, the test spider was placed in the petri dish and the arena was placed into the light-proof cabinet. After a 5-min settling-down period, the partition was removed. When the fly entered the dish defined the beginning of the test. As soon as the test began, the plunger was depressed so that neither the spider nor the fly could leave the petri dish. Tests lasted 15 min or until prey-capture, and were observed using IR video (see above). Type 4 tests are the closest approximation in the present study to the procedures used by Jackson (1977a) and Forster (1982b) to investigate non-visual predation in the salticids *Phidippus johnsoni* and *Trite planiceps*, respectively, but with the improvement of being able to observe the behaviour of spiders.

Sighted spiders tested on successive days in darkness and light (type 5 tests)

In type 5 tests, I assessed differences in the frequency with which spiders caught flies in darkness *versus* light. The testing procedure resembled type 1 tests except that spiders were not blinded. Each individual spider was tested once in the light and once in darkness on successive days (in random order). To begin tests in darkness, the tubes were placed horizontally in a light-proof cabinet as soon as the barrier was removed, and then left for 24 h. At the end of tests, dead flies were inspected for fang holes and mastication to confirm that they had been bitten.

RESULTS

Success at non-visual predation

Each of the 47 species tested (42 salticids and 5 non-salticids) caught prey in the absence of visual cues in at least one type of test (Tables 2-4). There was no evidence of interspecific differences among salticids in how frequently they caught prey in darkness during type 1, type 2 or type 5 tests (tests of independence, $P > 0.1$). However, there was significant interspecific variation among salticid species during type 3 tests using fruit flies and house flies (tests of independence: fruit flies $X^2 = 107.30$, $P < 0.001$; house flies; $X^2 = 116.80$, $P < 0.001$) and type 4 tests using house flies (test of independence, $X^2 = 160.10$, $P < 0.001$). All species of non-salticids caught flies in all types of test, and there was no evidence that they differed in capture frequency in any type of test (tests of independence, $P > 0.1$).

In type 5 tests, all salticids caught fruit flies and house flies less frequently in the dark than in the light (Table 4). In contrast, there was no evidence that absence of light affected how often *C. cambridgei*, the non-salticid spider tested, caught flies (Table 4).

Spiders sometimes caught flies immediately following first contact ('sudden captures'). In type 3 tests using fruit flies, sudden captures were made by the non-salticids *C. cambridgei* (16 of 24 captures recorded), *D. crocata* (2 of 10), *S. picta* (6 of 9) and *T. erebus* (4 of 8) as well as the salticids *E. parvula* (1 of 10), *H. minitabunda* (1 of 7), *M. dumicola* (1 of 4) and *Phidippus* sp.1 (1 of 5); in type 3 tests using house flies, sudden captures were made by the non-salticids *C. stratioticum* (3 of 11), *C. cambridgei* (19 of 45), *D. crocata* (2 of 13), and *S. picta* (6 of 16) as well as the salticids *C. canosa* (1 of 5), *E. parvula* (1 of 18), *Phidippus* sp. 2 (1 of 8), *P. africana* (1 of 4) and *T. planiceps* (5 of 18); in type 4 tests using house flies, sudden captures were made by the non-salticids *C. cambridgei* (8 of 20), *D. crocata* (3 of 10), and *S. picta* (4 of 15) and one salticid, *Trite planiceps* (9 of 37).

Association between spider aggressiveness and success at prey capture

There was variation among species in the frequency with which salticids confronted fruit flies and house flies when first contacted during type 3 tests (tests of independence: fruit flies, $X^2 = 70.34$, $P < 0.001$; house flies, $X^2 = 88.09$, $P < 0.001$), and house flies during type 4 tests (test of independence; $X^2 = 116.80$, $P < 0.001$) (see Table 3). That is, some salticid species were more inclined to confront flies than others. In contrast, all of the non-salticids were similar in that they usually confronted flies when first physically contacted (see Table 3), and there was no evidence of interspecific variation in frequency of confrontation by non-salticids during type 3 tests using fruit flies or house flies, or during type 4 tests using house flies (tests of independence, $P > 0.1$).

Salticid species that often confronted flies when first contacted tended to catch flies more frequently than species that rarely confronted flies in type 3 tests using fruit flies (Spearmans $r_s = 0.6677$, 13 *df*, $P < 0.01$) and house flies (Spearmans $r_s = 0.6779$, 16 *df*, $P < 0.01$), and type 4 tests using house flies (Spearmans $r_s = 0.5965$, 13 *df*, $P < 0.05$).

During type 3 tests with fruit flies, individual *T. auricoma* that confronted flies when first contacted were more likely to catch flies than individuals that did not confront flies (test of independence, $P < 0.05$). Otherwise, for all species used in type 3 and type 4 tests, there was no evidence that individuals that confronted flies when first contacted were more likely to catch flies than individuals of that species that avoided flies (tests of independence, $P > 0.1$).

Relationship between contacting and catching prey

The proportion of individuals that contacted fruit flies (a small, often immobile prey) during type 3 tests varied among salticid species (test of independence, $X^2 = 49.18$, 21 *df*, $P < 0.001$), but there was no evidence of interspecific variation in type 3 or type 4 tests in the

proportion of individuals that contacted house flies (a large, generally active prey) (tests of independence, $P > 0.1$). There was no evidence that the proportion of individuals of each species that contacted flies and proportion that caught flies in any test were correlated (Spearmans rank correlations, $P > 0.1$). For non-salticids, there was no evidence of interspecific variation for any test in the proportion of individuals that contacted flies (tests of independence, $P > 0.1$).

Absence of a relationship between spider size and capture success or aggressiveness

There was no evidence that the size of salticid species (see Table 1) and the proportion of individuals that caught flies was related in type 3 tests or type 4 tests (Spearmans rank correlations, $P > 0.1$). There was also no evidence that the size of salticid species and tendency to confront flies were related in type 3 tests or type 4 tests (Spearmans rank correlations, $P > 0.1$).

Comparison of type 3 and type 4 tests using house flies

For the following salticids, house flies were captured less frequently (tests of independence with Yates' correction) in type 4 tests (petri-dish arena) than in type 3 tests (tube arena): *Cosmophasis* sp. ($P < 0.05$), *E. parvula* ($P < 0.001$), *H. minitabunda* ($P < 0.001$), *M. marina* ($P < 0.001$), *M. mormon* ($P < 0.05$), *P. labiata* ($P<0.001$), *P. shultzi* ($P < 0.05$), *T. auricoma* ($P < 0.05$) and *T. planiceps* ($P < 0.05$). However, there was no evidence for any non-salticid species that frequency of prey-capture by was different in type 3 and type 4 tests (for all species, $P > 0.1$).

Table 2. Number of individuals tested (N) and percentage that captured flies (C) in type 1 and type 2 tests

	type 1 tests		type 2 tests	
	N	C	N	C
Tests using fruit flies				
Clubiona cambridgei[1]	9	66	6	66
Bavia aericeps	12	17	-	-
Corythalia canosa	9	22	-	-
Cosmophasis micarioides	6	17	-	-
Epeus sp.1	7	14	-	-
Euophrys parvula	12	33	-	-
Hasarius adansoni	8	13	-	-
Helpis minitabunda	8	24	-	-
Holoplatys sp.	7	0	9	22
Jacksonoides queenslandica	10	0	14	14
Lyssomanes viridis	10	0	11	9
Marpissa marina	7	0	7	14
Mopsus mormon	10	10	-	-
Myrmarachne lupata	6	0	5	20
Phidippus johnsoni	12	0	11	9
Plexippus calcarata	11	27	-	-
Portia labiata	7	0	8	13
Tauala lepidus	6	17	-	-
Thiania bhanoensis	7	14	-	-
Trite auricoma	15	20	-	-
Trite planiceps	10	40	7	43
Zendora orbiculata	6	17	-	-
Tests using house flies				
Clubiona cambridgei[1]	4	100	-	-
Bavia aericeps	5	20	-	-
Euophrys parvula	5	20	-	-
Helpis minitabunda	4	0	5	20
Jacksonoides queenslandica	9	0	10	20
Marpissa marina	8	38	7	14
Mopsus mormon	4	25	-	-
Phidippus johnsoni	5	0	10	10
Tauala lepidus	7	43	-	-
Trite auricoma	8	38	-	-
Trite planiceps	10	40	-	-

[1] A non-salticid

Table 3. Results of type 3 and type 4 tests

	N	Contact[2]	Confront[3]	Capture[4]
Type 3 tests using fruit flies				
Cheiracanthium stratioticum[1]	28	50	86	50
Clubiona cambridgei[1]	33	73	92	73
Dysdera crocata[1]	18	72	62	56
Supunna picta[1]	15	73	82	60
Taieria erebus[1]	16	63	70	50
Bavia aericeps	15	73	9	0
Corythalia canosa	17	53	0	12
Cosmophasis bitaeniata	4	75	33	50
Cosmophasis sp.	12	83	0	42
Epeus sp.2	3	67	0	0
Eris marginata	5	100	0	0
Euophrys parvula	22	64	57	45
Helpis minitabunda	46	87	8	15
Holoplatys planissima	8	50	25	0
Jacksonoides queenslandica	20	80	0	0
Lyssomanes viridis	33	70	0	12
Marpissa marina	28	93	23	46
Mogrus dumicola	26	42	9	15
Mopsus mormon	8	88	14	0
Phidippus sp.1	13	85	45	38
Phidippus sp.2	9	89	13	33
Portia fimbriata	22	64	0	5
Portia labiata	64	53	3	5
Tauala lepidus	13	77	40	46
Trite auricoma	38	53	25	18
Trite planiceps	43	72	43	63
Zendora orbiculata	2	50	100	0
Type 3 tests using house flies				
Cheiracanthium stratioticum[1]	13	85	90	85
Clubiona cambridgei[1]	54	93	89	83
Dysdera crocata[1]	15	100	85	87
Supunna picta[1]	18	100	88	89
Bavia aericeps	15	100	7	13
Corythalia canosa	17	94	38	29
Cosmophasis sp.	16	88	14	38
Epeus sp.2	7	100	0	57
Eris marginata	5	100	0	0
Euophrys parvula	22	95	43	82
Helpis minitabunda	50	100	6	34
Holoplatys planissima	12	92	20	25
Jacksonoides queenslandica	16	94	7	0

Lyssomanes viridis	42	98	3	14
Marpissa marina	32	94	50	56
Mogrus dumicola	26	96	28	46
Mopsus mormon	10	80	0	40
Phidippus sp.1	14	100	38	100
Phidippus sp.2	9	100	13	89
Portia africana	7	86	17	57
Portia fimbriata	26	100	0	12
Portia labiata	24	83	11	33
Portia shultzi	10	100	20	50
Tauala lepidus	16	100	19	25
Trite auricoma	33	91	21	27
Trite planiceps	21	100	70	86
Type 4 tests using house flies				
Clubiona cambridgei[1]	22	91	85	91
Dysdera crocata[1]	12	100	67	83
Supunna picta[1]	16	94	87	94
Bavia aericeps	15	93	0	0
Corythalia canosa	15	87	0	7
Cosmophasis sp.	14	86	8	0
Epeus sp.	9	89	0	11
Euophrys parvula	46	85	0	0
Helpis minitabunda	39	95	5	3
Holoplatys planissima	4	100	0	0
Jacksonoides queenslandica	20	85	0	0
Lyssomanes viridis	35	94	0	9
Marpissa marina	26	100	4	4
Mopsus mormon	12	83	0	0
Portia africana	5	100	0	0
Portia labiata	66	89	0	0
Portia shultzi	10	100	0	0
Tauala lepidus	12	83	20	17
Trite auricoma	36	92	9	3
Trite planiceps	70	90	44	53

[1] A non-salticid

[2] Percentage of N that contacted the fly (see text)

[3] Percentage of individuals that confronted the fly (see text) immediately after first contact

[4] Percentage of N that captured the fly

Table 4. Conditions under which spiders caught flies during type 5 tests and whether spiders more frequently caught fruit flies in light than in darkness

	Light only	Dark only	Both	Neither	McNemar [2] *P*
Tests using fruit flies					
Clubiona cambridgei[1]	2	3	10	3	NS
Asemonea tenuipes	7	0	2	1	0.01
Bavia aericeps	15	0	1	2	0.001
Corythalia canosa	10	0	1	4	0.005
Cosmophasis micarioides	14	0	2	3	0.001
Cosmophasis bitaeniata	5	0	2	4	0.05
Cyrba ocellata	6	0	1	3	0.025
Euophrys parvula	17	0	3	5	0.001
Epeus sp.2	18	0	1	2	0.001
Eris marginata	11	0	4	0	0.001
Euryattus sp.	9	0	3	4	0.005
Hasarius adansoni	13	1	3	3	0.005
Helpis minitabunda	17	1	2	2	0.001
Hentzia mitrata	5	0	2	1	0.05
Holoplatys sp.	19	0	4	3	0.001
Jacksonoides queenslandica	20	0	4	4	0.001
Lyssomanes viridis	15	0	0	4	0.001
Marpissa marina	18	1	2	3	0.001
Menemerus bivattatus	12	0	3	5	0.001
Mopsus mormon	13	0	2	5	0.001
Myrmarachne lupata	19	1	3	2	0.001
Natta rufopictus	14	1	2	3	0.001
Phidippus johnsoni	18	0	0	3	0.001
Plexippus calcarata	17	0	3	1	0.001
Portia labiata	9	2	0	11	0.05
Simaetha paetula	19	0	3	1	0.001
Tauala lepidus	12	1	3	1	0.005
Thiania bhanoensis	22	1	2	2	0.001
Thorella ensifera	11	1	2	2	0.005
Trite auricoma	19	0	6	1	0.001
Trite planiceps	16	0	8	1	0.001
Tularosa plumosa	5	0	2	2	0.05
Viciria praemandibularis	13	0	3	4	0.001
Zendora orbiculata	15	0	1	3	0.001
Tests using house flies					
Clubiona cambridgei[1]	0	2	5	1	NS
Bavia aericeps	8	0	2	0	0.005
Euophrys parvula	5	0	2	1	0.05
Helpis minitabunda	7	1	0	6	0.05

Jacksonoides queenslandica	8	0	1	1	0.005
Marpissa marina	9	0	2	0	0.005
Mopsus mormon	5	0	2	0	0.05
Phidippus johnsoni	8	0	2	1	0.005
Plexippus calcarata	6	0	1	1	0.025
Tauala lepidus	5	0	2	0	0.05
Trite auricoma	4	0	1	3	0.05
Trite planiceps	8	0	4	0	0.005

[1] A non-salticid

[2] Only columns 'Light only' and 'Dark only' relevant for McNemar tests for significance of changes (Sokal & Rohlf, 1981)

Also, some salticids confronted house flies less frequently in type 4 tests than in type 3 tests: *C. canosa* ($P < 0.05$), *E. parvula* ($P < 0.001$), and *M. marina* ($P < 0.001$). However, there was no evidence for any non-salticid species that frequency of confrontation was different in type 3 and type 4 tests nor was there evidence that frequency of contact with house flies was different in type 3 and type 4 tests for any salticid or non-salticid (for all species, $P > 0.1$).

Prey-capture behaviour in the absence of visual cues

Salticids always lunged to catch prey, and were never observed to leap onto prey as they commonly do in light. No salticid or non-salticid ever lunged at the flies prior to being physically contacted. *Cheiracanthium stratioticum* and *C. cambridgei*, non-salticids, sometimes chased after flies that moved away following contact, but no salticid ever did this.

Sometimes, after lunging at flies, salticids held the flies for 1-5 s with their fangs whilst appearing to make little or no attempt at using their legs to grasp the fly. In these instances, flies broke free or were released by the spiders but always stopped moving within 10 min of being bitten. During type 3 tests, the following salticids made bite-then-release attacks on house flies: *B. aericeps* (1 of 2 captures recorded), *C. canosa* (1 of 5), *H. minitabunda* (1 of

17), *M. dumicola* (2 of 12), *M. mormon* (1 of 4), *Phidippus* sp.1 (2 of 14), *P. labiata* (1 of 8), *T. auricoma* (3 of 9) and *T. planiceps* (2 of 18). After these attacks, spiders picked up the immobilised fly and ate it, the only exception being *B. aericeps*. *Trite planiceps* was the only salticid observed to kill a fruit fly by a bite-then-release attack during type 3 tests (3 of 27). In type 4 tests using house flies, spiders always held onto the flies until they died.

DISCUSSION

The present study finds that, as well as being adept visual predators (Dill 1975; Forster 1977a), many salticids are able to catch prey when denied visual cues. However, the present study is limited to the laboratory; whether and how they use the ability to catch prey in the absence of visual cues in nature remains largely unstudied. Here I briefly discuss naturally occurring situations in which salticids might depend primarily on cues other than vision to coordinate offensive or defensive actions.

Use of senses other than vision when hunting

By emphasising the role of vision, qualitative accounts describing the typical predatory sequences of salticids (e.g., Drees 1952; Forster 1977a) have not addressed the issue of how salticids deal physically with struggling prey. Yet, holding onto and subduing prey is an important aspect of hunting, especially for salticids that attack relatively large or dangerous prey (Robinson & Valerio 1977; Jackson & Hallas 1986a; Jackson & McNab 1989a). Once in contact with prey, vision would be of little use and non-visual cues, especially tactile cues, are probably of primary importance. Possibly, this role for non-visual cues after contact with the prey predisposes salticids to being able to catch prey in the dark, even if they never catch prey in darkness in nature. That is, non-visual predation in the laboratory may be an artifact.

However, consideration should also be given to the possibility that salticids sometimes hunt at night when visual cues would not be available during any part of the hunt (see Reiskind 1982). Most salticid species are cursorial hunters (i.e., do not live in webs) and their exceptional eyesight allows them to organize attacks on prey from a distance. At first, it may seem unlikely that a cursorial salticid could be an effective predator at night. However, a variety of spiders from other families are successful cursorial hunters, both during the day and at night, despite having simple eyes and lacking acute vision ('short-sighted hunting spiders'). There is no obvious reason why salticids should not also be able to hunt at night relying upon senses other than their acute vision.

As well as the typical cursorial salticids, there are some species that build webs (Jackson & Hallas 1986a; Jackson & Pollard 1990) or web-like nests (Hallas & Jackson 1986a,b), or shelter overnight in webs built by other species (Jackson & Willey 1994). Web-building and web-invading spiders from other families lack acute vision, and instead use their webs as extensions of their tactile sense organs to hunt both during the day and at night (Witt 1975; Suter 1978; Jarman & Jackson 1986). Nocturnal foraging by web-dwelling salticids has not been investigated, but there is no obvious reason why they could not, like web-dwelling spiders from other families, use tactile cues from webs to hunt at night.

Also, nocturnal predation is not the only context in which hunting in the absence of visual cues may be relevant because some salticids have habits that pre-dispose them to encounters with potential prey in dark places even during the day. Many salticids take shelter during times of inactivity during the day in dark places such as under rocks and bark or inside rolled-up leaves (Forster 1979; Hallas & Jackson 1986b) and may encounter potential prey at these sites. Whether salticids sometimes hunt at these dark sites during the day has not been investigated, but the present study suggests that this is likely.

Use of senses other than vision when defending against predators

Although predation is conventionally envisaged as a means of gaining food, killing another animal may also function in other ways, including as a defense against the predator's own predators (Curio 1976; Archer 1988). If a predator later eats the enemy it kills, attributing a function to the kill may be difficult. For salticids in the dark, attacking another animal, even a fly, might primarily reflect an anti-predator adaptation ('active defense'), with getting a meal an incidental bonus of successful defense.

In common with spiders from other families (Coville 1987; Wise 1993), most salticids are probably prone to attacks by diurnal predators such as sphecid and pompilid wasps, and other spiders, including conspecifics (Jackson 1980c; Jackson & McNab 1989b; Jackson *et al.* 1990). If a salticid is attacked by a previously undetected fast-moving predator in daylight, it would often be unable to make more than cursory visual assessment of its attacker before being physically contacted and having to respond. This situation would lead to favouring of an ability to use other cues, such as physical contact, to release appropriate defensive behaviour such as fleeing, threatening, or orienting, grasping, and killing the attacker.

Most salticids are probably also prone to attacks by predators, such as other hunting spiders, while in their nests at night (e.g., Jackson 1976; Jarman & Jackson 1986) or while sheltering in dark places during the day. When these attacks happen, a salticid might often be forced to defend itself in the absence of visual cues from the attacker. Even salticids that build their nests in well-lit situations may be denied use of visual cues to defend themselves against diurnal predators, as their view would be obscured by the opaque walls of the nest (see Hallas & Jackson 1986b).

There is very little information from the field about what predators attack salticids in their nests at night or during the day, how salticids respond to attacks, and how successful

salticids are at defending themselves or fleeing, but infra-red video technology, such as has been used in the present study, offers previously unavailable opportunities to investigate this.

Interspecific differences in non-visual predation

The poorly known natural histories of most salticid species, including those used in the present study, cause difficulty in interpreting the observed interspecific differences in predation success and aggressiveness toward flies in darkness. However, the clear positive association between capture success and aggressiveness suggests some hypotheses about patterns in nature. Species that only rarely caught or confronted flies in the present study might tend to flee in nature when contacted in the absence of visual cues. These species might rarely be able to defend themselves against enemies or catch potential prey when denied visual cues in nature. In contrast, species that often caught (and confronted) flies in the present study might, in nature, be more prone and able to defend themselves actively, and may also be those species for which non-visual foraging is the most important.

That no clear relationship was detected between spider size and aggressiveness or capture frequency is likely a consequence of restricting testing to spiders that were observed catching each prey in light; many small species that might have been especially unlikely to catch house flies in darkness were omitted because they had failed to catch them in light. It is very likely that size does in fact largely determine ability to catch prey. Species differences in frequency of contact with fruit flies in type 3 tests suggests a possible role for species differences in motility as an influence on capture success in these tests.

Trite planiceps, the salticid for which non-visual predation was first reported by Forster (1982b), appears to be a special case with respect to predation in the absence of visual cues. Although many other species of salticid often caught house flies when tested in tubes, *T.*

planiceps was unusually aggressive and unusually successful at prey capture when tested in the more spacious petri-dishes. Perhaps, as was suggested by Forster (1982b), *T. planiceps'* unusual predatory behaviour is an adaptation related to frequent encounters with potential prey, dangerous intruders, or both in the dark recesses within rolled-up leaves where this species normally lives. *Trite planiceps* used in the present study share their habitat with nocturnal enemies, including the large, aggressive clubionids, *Clubiona cambridgei* and *Cheiracanthium stratioticum,* and *Taieria erebus*, an araneophagic gnaphosid with venom that appears to be especially effective against other spiders (Jarman & Jackson 1986). Each of these common hunters has been observed feeding on *T. planiceps* adults and juveniles in nature (unpublished data). Of course, other salticids tested must also encounter enemies in darkness (Jackson 1976; Jarman & Jackson 1986), but the abundance of nocturnal hunting spiders and confining microhabitat inside rolled-up leaves and may make encounters with predators unusually frequent and unusually difficult to flee from.

CHAPTER 5

Brood-defense as a function of maternal brood-attendance in *Trite planiceps* Simon (Araneae, Salticidae)

ABSTRACT

In support of the hypothesis 'brood-attendance by maternal jumping spiders (Salticidae) functions as brood-defense', broods of *Trite planiceps* are shown to suffer increased predation in nature when maternal females are removed. Apparent predators of unattended *T. planiceps* broods are identified in nature, and that these species eat *T. planiceps* eggs and post-embryos is confirmed in the laboratory. *Trite planiceps* males and females not attending broods of their own ate the eggs and post-embryos of conspecifics in the laboratory but females with their own broods did not; predation of conspecific's broods appears to be suppressed by maternity. If starved, however, maternal *T. planiceps* females did sometimes eat their own or conspecific's broods, indicating that maternal supression of oophagy is incomplete and is conditionally dependent on hunger.

INTRODUCTION

Although some spiders typically abandon their eggsacs soon after oviposition, others stay with them until the juveniles disperse (Foelix 1982). 'Brood-attendance' by maternal females is widespread in jumping spiders (Salticidae), but the function of this behaviour in salticids has rarely been studied. Richman & Jackson (1992) have suggested that, like some spiders from other families (e.g., Pollard 1984; Willey & Adler 1989; Horel & Gundermann

1992), brood-attendance by maternal salticids functions as brood-defense. But Richman & Jackson's (1992) suggestion is presently supported by only indirect evidence from nature and laboratory studies (Eberhard 1974; Jackson & Willey 1994), and whether brood-attendance by maternal salticids reduces the frequency of predation on broods does not appear to have been investigated for any species.

Trite planiceps Simon is a common New Zealand salticid that appears especially well-suited to an investigation of whether maternal brood-attendance can reduce the frequency of predation on broods. Most salticids shelter and oviposit inside a dense, opaque, silken cocoon (Hallas & Jackson 1986a). For these species, it is very difficult to assess incidence of predation on the brood without damaging the cocoon and thereby increasing exposure to predation or damage from other sources. *Trite planiceps* usually does not shelter or oviposit within such a cocoon; this species instead deposits its eggs in layers that form an open platform within the cavities formed by rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants (Forster 1977a). The developing offspring of *T. planiceps* are clearly visible through the thin sheet of silk that covers them. When leaves containing broods are un-rolled, the maternal females are found standing on their nests facing the entrance to the rolled-up leaf (Chapter 2, Fig. 6). In the present study, I investigate the hypothesis 'brood-attendance by maternal *T. planiceps* functions as brood-defense' and identify some of the predators that might eat unattended broods.

MATERIALS AND METHODS

Effects of maternal brood-attendance on survivorship of broods in nature

Ninety *Trite planiceps* broods with attendant females were located in rolled-up leaves of New Zealand flax near Christchurch, New Zealand. All broods contained 1-3 egg-batches (eggs deposited at the same time and enclosed by thin sheets of silk) when experiments began, and each egg-batch contained 8-20 eggs or post-embryos. No broods contained first instar spiderlings (dispersing stage) when experiments began.

Forty-five broods were randomly assigned to each of two experimental groups: 'un-attended' and 'attended'. Maternal females were removed from broods in the un-attended group, but were left on the broods of the attended group. Each rolled-up leaf containing a brood was marked with enamel paint for relocation and individual identification. All broods were initially located, and experiments started, between 20 November and 11 December 1993. Broods were checked for a maximum of 6 weeks, the maximum latency from oviposition to dispersal of juveniles observed in nature during preliminary assessments.

To inspect a brood, the rolled-up leaf was carefully un-rolled to expose the nest. When the leaf was unrolled, the maternal female usually retreated to a part of the leaf that remained rolled-up and returned to the nest later. Broods were inspected once weekly to assess whether females were present on broods in the attended group, and to assess broods for evidence of predation. Each week, the number of eggs and post-embryos in the uppermost egg-batches were counted. Absence of eggs or post-embryos that were present the previous week and physical damage to the nest was adjudged to be evidence of predation. Assessment excluded first-instar spiderlings for which it was not possible to ascertain whether disappearance was due to dispersal or predation. After inspection, the leaves rolled back to their original shape.

Inspections were always carried out within 2 h of sunset, as preliminary observations

found that maternal females that leave the rolled-up leaf containing the brood during the day usually returned within several hours before darkness. Dusk was therefore the most reliable time to assess whether nests in the attended group still had an attendant female. Broods were omitted from analysis if the leaves were damaged during sampling, and attended broods were omitted if maternal females went missing (never subsequently observed with the brood). To assess the effect of maternal brood-attendance on frequency of predation on broods, I compared the cumulative frequencies of predation since the previous weekly inspection for attended and unattended broods, the likelihood that a nest suffered any predation in the testing period, and the likelihood that at least some offspring survived until the end of the 6-week assessment period.

Predation on *T. planiceps* broods the laboratory

Species suspected to be predators of *T. planiceps* broods in nature were collected, and whether they eat undefended broods was investigated in the laboratory. Individual adults of each suspected predator were maintained in the laboratory for 1-2 weeks prior to testing following procedures outlined by Jackson & Hallas (1986a). They were given *ad libitum* access to house flies (*Musca domestica* L.) and fruit flies (*Drosophila melanogaster* Meigen) as prey.

Gravid *T. planiceps* females (evident from distended abdomens) were also collected and maintained in the laboratory. After a *T. planiceps* female had deposited 2 or 3 batches of eggs and the nest contained both eggs and post-embryos, the maternal female was removed from her cage and a suspected brood-predator was released into the cage containing the brood. Whether any eggs or post-embryos had been eaten was checked 7 days later.

RESULTS

Effects of maternal brood-attendance on survivorship of broods in nature

The presence of maternal *Trite planiceps* on broods was strongly associated with reduced frequency of predation on broods. Some eggs of broods in the unattended group were found to have been eaten since the previous week in 66 (31.6 %) of 209 sampling events, whereas some eggs of broods in the attended group were found to have been eaten since the previous week in only 8 (3.3 %) of 240 sampling events (test of independence with Yate's correction, $X^2 = 64.75$, $P < 0.001$).

Of the 38 broods that were attended throughout the 6-week period (maternal females went missing from 5 broods, and 2 broods were omited because the leaves split open during sampling), only 7 (18 %) suffered any instances of predation. In contrast, 35 (78 %) of the 45 unattended broods suffered one or more instance of predation (test of independence with Yate's correction, $X^2 = 26.71$, $P < 0.001$). Some offspring from all broods attended throughout the 6-week period survived to the end of the testing period, but some offspring survived this long in only 8 (18 %) of the 45 unattended broods (test of independence with Yate's correction, $X^2 = 53.10$, $P < 0.001$).

The clubionid spiders *Clubiona cambridgei* and *Cheiracanthium stratioticum*, and the gnaphosid spider *Taieria erebus*, were commonly seen in rolled-up leaves similar to those in which *T. planiceps* nests were usually found. Each of these nocturnal hunters was sometimes found in the remains of unattended *T. planiceps* broods that had suffered predation, although they were never actually observed eating eggs of *T. planiceps* in nature. An earwig, *Forficula auricularia* (Dermaptera, Forficulidae), was found on unattended broods that had suffered predation on 11 occasions, and on 3 of these occasions was observed eating eggs. Adult female *T. planiceps* were found on unattended broods on 15 occasions. On 11 of these occasions,

some of the brood had been eaten. In 3 cases, the *T. planiceps* female apparently adopted the nest, depositing her own eggs alongside those already present.

Predation on *T. planiceps* broods in the laboratory

All of the suspected predators that were found in damaged nests in nature ate the eggs and post-embryos of *T. planiceps* in the laboratory (Table 1). Because none of the predators discriminated between eggs and post-embryos, data for these prey types have been pooled.

When well-fed, *T. planiceps* males and females without broods of their own ('non-brooding females') ate eggs and post-embryos, but females with broods of their own ('brooding females') did not eat each other's broods. When well-fed, non-brooding females were more likely to eat eggs deposited by conspecific females than were brooding females on conspecific's eggs (test of independence, $X^2 = 7.94$, $P < 0.01$) or on their own eggs (test of independence, $X^2 = 13.85$, $P < 0.001$) (Table 1). Brooding females (test of independence, $X^2 = 6.86$, $P < 0.01$) and females on their own eggs (test of independence, $X^2 = 6.90$, $P < 0.01$) more frequently ate eggs when they were starved than when they were well-fed (Table 1).

DISCUSSION

In support of Richman & Jackson's (1992) suggestion that brood-attendance by maternal salticids functions as brood-defense, the present study found that *Trite planiceps* broods deprived of maternal females suffer greatly increased mortality from predation. Under natural conditions, maternal females that abandoned their broods altogether, or spent insufficient time guarding, would suffer greater losses from brood predation than more attentive conspecifics.

Table 1. Number of individuals tested for predation on *Trite planiceps* broods in the laboratory, and percentage that ate one or more eggs or post-embryos during the 7-day testing period. 'Brooding females' are attending broods of their own whereas 'non-brooding females' had not attended broods for at least 10 days prior to testing.

	N	%
C. cambridgei female	10	90
C. stratioticum female	10	100
T. erebus female	10	100
F. auricularia	10	70
T. planiceps male	10	50
T. planiceps brooding female (conspecific's brood)	16	0
T. planiceps brooding female (own brood)	30	0
T. planiceps starved brooding female (conspecific's brood)	14	36
T. planiceps starved brooding female (own brood)	14	21
T. planiceps non-brooding female	15	40

Although this is the first direct evidence from nature, there is ample reason to suspect that brood-attendance also functions as brood-defense in other salticids. Salticids commonly share their habitats with ants, parasitic hymenoptera, diptera, mantispids, spiders, and various opportunistic scavengers (e.g., Dermaptera) that might attack their broods (Austin 1985; Jackson & Hallas 1986a; Jarman & Jackson 1986; Nyffeler *et al.* 1990). Additionally, like *T. planiceps*, the broods of some salticids might be prone to attack by foraging conspecifics (although suppression of brood-predation by maternity may lessen this threat). With their fangs and venom, weapons otherwise employed when hunting, maternal salticids would probably present a formidable deterrent for many prospective brood predators.

In accord with a general paucity of information about salticid life-histories, little is known about how salticids detect and deal with enemies at their nests. In a rare exception, Eberhard (1974) describes maternal *Lyssomanes jemineus* physically repelling diurnal intruders from the surface of their nests. In this case, the salticid could use its exceptional acute vision (Blest *et al.*, 1990) to recognise intruders and mediate attacks. But many of the predators reported to eat salticid broods are nocturnal (Jackson 1976; Jarman & Jackson 1986), attacking when the salticid's acute vision would be redundant. All of the hetero-specific predators of *T. planiceps* broods identified in this study are active at night. Additionally, maternal salticids attacked at their nests during the day may be unable to see the attacker because their view would be obscured by the silken cocoon or because, like *T. planiceps*, they build their nests in dark places (Hallas & Jackson 1986a). How salticids detect and deter potential brood-predators when visual cues are absent warrants special attention as an unusual instance in which salticids are active whilst restricted to the sensory limits of spiders lacking acute vision.

Nest discrimination and incomplete suppression of oophagy

Spiders do not usually eat their own eggs, and there is evidence that oophagy is suppressed by maternity in some species (Pollard 1984; Fink 1987; Horel & Gundermann 1992). *Trite planiceps* females appear to have behavioural flexibility in tendency to eat or guard eggs, with decision rules based on a trade-off between nutrition and brood-defense. This behavioural flexibility comprises two disparate options, eating and guarding eggs, with the option chosen depending on hunger.

Trite planiceps females readily adopted conspecific' broods; this species appears unable to discriminate between own and foreign eggsacs and uses a general suppression of intraspecific oophagy when maternal to avoid eating their own eggs (see Horel & Gundermann 1991). But this general suppression excludes conspecifics eggs as a food source at a time when such a rich food may be especially useful for the production of more eggs. In contrast, *Portia labiata*, another salticid, has a more complex mechanism for suppression of oophagy. *Portia labiata* is able to discriminate between own and foreign eggsacs and can therefore eat conspecific's eggs even when guarding their own broods (Clark & Jackson 1994b). But *P. labiata* is a web-invading araneophage for which victim's eggs may be an important food (see Jackson & Hallas 1986a). *Trite planiceps'* simple, but crude, mechanism likely reflects a comparatively low dependence on eggs as a source of nutrition.

SECTION II

Functional conflicts and appendotomy.

CHAPTER 6

Costs of an antipredator tactic: appendotomy reduces fighting ability in *Trite planiceps* (Araneae, Salticidae)

ABSTRACT

Trite planiceps (Salticidae) males and females use Legs I extensively for visual and tactile signalling during intrasexual contests. In nature, however, spiders are often found missing one, or even both, of these legs; I here show that absence of Legs I alters both fighting ability and behaviour during contests. In laboratory experiments, *T. planiceps* males and females that were missing one or both Legs I tended to lose contests against same-sized intact rivals. During contests between spiders that differed both in size and number of Legs I missing, these two variables interacted as combined determinants of fighting ability. Spiders that were missing Legs I did not use other legs for visual displays but tended to move more frequently than their rivals. Additionally, females that were missing both Legs I leaped at rivals more frequently than did females that were intact or missing only one Leg I. Increased motility and frequency of leaping is interpreted as compensation for absence of legs. When contests escalated to apparent physical 'tests of strength', both males and females missing Legs I often used Legs II to perform behaviours involving Legs I in intact spiders. The likely reasons for reduced fighting ability in spiders that have appendotomized legs and the trade-offs between benefits of appendotomy as an anti-predator tactic and costs caused by reduced fighting ability are discussed.

INTRODUCTION

In nature, spiders are often found with one or more legs missing or distinctly smaller than usual (Roth & Roth 1984; Vollrath 1990). Although some spiders discard ('appendotomize': Roth & Roth 1984) limbs if they have difficulty discarding the old exoskeleton during moulting (Foelix 1982), the absence of legs is usually attributed to appendotomy of appendages that had been grasped or envenomated by dangerous opponents (Savory 1964; Randall 1981; Eisner & Camazine 1983).

The antipredator tactic of appendotomizing legs provides spiders with the immediate benefits of avoiding more serious injury or even death (Formanowicz 1990). However, these benefits may be somewhat diminished by various costs including nutritional investment in healing wounds, regenerating new appendages, and reduced efficacy during the activities for which intact spiders use their legs. The benefits gained by appendotomy are countered by various costs in a wide range of taxa including lizards (Arnold 1984), crustaceans (Conover & Miller 1978; Berzins & Caldwell 1983; Smith 1992), and insects (Dixon 1989; Carlberg 1992), as well as in agelenid, thomisid and lycosid spiders (Hammerstein & Riechert 1988; Dodson & Beck 1993; Uetz, Miller & McClintock unpublished data). However, whether such costs exist for jumping spiders (Salticidae) does not appear to have been investigated. This study is a first step toward understanding the potentially conflicting selection pressures surrounding the antipredator tactic of appendotomizing legs in jumping spiders (Salticidae).

Trite planiceps, a common New Zealand salticid, appears commonly to use the antipredator tactic of appendotomy. During collecting for related studies, I found that 11.1% of 223 males, 13.8% of 465 females and 6.3% of 236 juveniles collected over three years were missing one of their Legs I. Approximately 1% of males, females and juveniles were missing both Legs I. Appendotomy of Legs I at moulting was not observed during laboratory-rearing

of 167 *T. planiceps* juveniles to adulthood (unpublished data), and so these legs were almost certainly lost in the context of anti-predator defense. As well as conspecifics, *T. planiceps* shares its habitat with numerous clubionid and gnaphosid hunting spiders against which such defense might often be necessary (see Chapter 5).

Like many other salticids (Crane 1949; Jackson 1982a; Richman & Jackson 1992), males and females of *T. planiceps* use Legs I extensively during intrasexual contests for a complex array of visual and tactile displays (Chapter 2). Appendotomy of limbs causes a reduction in the fighting ability of some stomatopods (Berzins & Caldwell 1983), crabs (Smith 1992), and snapping shrimps (Conover & Millar 1978), as well as in spiders from other families (Hammerstein & Riechert 1988; Dodson & Beck 1993; Uetz Millar & McClintock unpublished data). Jackson & Hallas (1986a) speculate that *Portia* spp. (Salticidae) that have lost legs might be disadvantaged during intrasexual contests, but whether appendotomy reduces fighting ability in salticids appears not to have been investigated.

In this chapter, I investigate (1) whether *T. planiceps* that have appendotomized Legs I are disadvantaged during intrasexual contests, (2) whether absence of Legs I and size interact as determinants of fighting ability and (3) whether *T. planiceps* compensates behaviourally for disadvantages caused by the absence of Legs I.

MATERIALS AND METHODS

Collection and maintenance of spiders

Adult males and females of *T. planiceps* were collected from a population living in New Zealand flax (*Phormium tenax*) near Christchurch, New Zealand. All spiders were maintained using standard methods (Jackson & Hallas 1986a) and were provided *ad libitum* access to house flies (*Musca domestica* L.) as prey. Maximum cephalothorax width was used as a

measure of size (see Chapter 2). To minimize variation in the condition of females as a consequence of reproductive state, females were collected and tested in the period June-August, 2-3 months before the reproductive season (unpublished data).

The following terminology is used: 'intact' spiders have both Legs I, 'injured' spiders are missing one or both Legs I, 'less-injured' spiders have more Legs I than rivals, and 'more-injured' have fewer Legs I than rivals.

Question 1. Does appendotomy of Legs I reduce *T. planiceps*' fighting ablity?

If appendotomy of Legs I reduces fighting ability, then spiders that have appendotomized one or both legs I should lose tend to contests against intact rivals that are equal in other respects. Also, spiders missing both Legs I should tend to lose when matched in contests against rivals that are equal in all respects except that they are missing only one Leg I. Relative size of rivals is known to be a good predictor of the outcome of male-male and female-female contests in *T. planiceps* (Chapter 2). To investigate the effects of appendotomising Legs I on fighting ability, I staged contests between equal-sized, same sex spiders that differed in the number of Legs I that had been appendotomized.

The measured spiders were sorted into groups comprising three spiders that differed in size by less than 3%. Each member of each group was then assigned randomly to one of three treatments ('intact', 'missing one Leg I', and 'missing both Legs I') so that each group of three spiders then contained one individual in each of the three treatments. If only two spiders of any particular size were available, groups of two spiders randomly assigned to two different treatments were used.

To ensure that spiders were in healthy condition, they were maintained in the laboratory for 10-14 days before Legs I were removed. To remove a spider's Leg I, the femur of the leg

being removed was held with forceps until the spider discarded the leg to escape. Spiders always discarded legs at the coxa-trochanter joint and often did not discard legs unless the exoskeleton was broken by the pressure of the forceps. For spiders in the treatment 'missing one Leg I', a Leg I was randomly selected for removal. For spiders in the treatment 'missing both Legs I', both Legs I were removed within 2 h. All spiders were then maintained for a further 10-14 days to recover before being used in experiments.

The testing arena and procedures were as for encounters 'in light' in Chapter 2. Each member of each group was tested once in contests against each other member of its equal-sized group. Different pairings of spiders from each group of spiders were randomly selected for testing on subsequent days. Spiders were used only once for each type of test (e.g., intact *vs.* one Leg I missing) and were never used in experiments more than once per day. All interactions were video-recorded and analysed later.

Question 2. Do absence of Legs I and size interact as determinants of fighting ability?

If *T. planiceps* uses both relative size and relative number of legs missing to resolve contests, then the size-advantage required to beat less-injured rivals should give a quantitative estimate of the disadvantage caused by appendotomy.

Spiders used in the experiment examining effects of appendotomy during contests between equal-sized rivals were later used in these experiments. Additional spiders of various sizes that were intact, missing one or missing both Legs I, and had been maintained in the same way as spiders in equal-sized groups, were also used in this experiment. Spiders of different size and injury state were randomly paired with the provisos that the more-injured spider was 0.80-1.20 times the size of the less-injured spider and that no spider was used more than three times for any of the three classes of pairing (e.g., intact *vs.* missing one Leg I). Procedures

were otherwise identical to the experiment using same-sized spiders.

Question 3. Do *T. planiceps* compensate behaviourally for absence of Legs I?

For all interaction types, I recorded whether spiders missing Legs I used other legs to perform behaviours for which intact spiders used Legs I. A complete account of the behaviour used by *T. planiceps* during intra-sexual contests is presented in Chapter 2.

Locomotory movement appears to be an important part of agonistic display in *T. planiceps*. With some movements, such as charging and leaping at rivals, the spider appears to threaten its rival with a mock attack. Spiders missing Legs I may compensate by making more frequent locomotory movements during contests either as a threat, or as a means of becoming a harder target for rivals to attack (a 'protean defense'; Humphries & Driver 1967). To check this, I compared the frequency of locomotory movements (total number of movements divided by interaction duration) by spiders during all interaction types, pooling data from symmetric (same-sized rivals) and asymmetric (different-sized rivals) contests.

Question 4. Does appendotomy influence contest duration or maximum esalation?

If it is more difficult for spiders to assess and compare fighting ability when Legs I are absent, then contests involving spiders missing Legs I might last longer or escalate higher than contests between intact spiders before resolution. Contest durations and whether contests escalated to embracing were recorded and compared for all contests, pooling results of symmetric and asymmetric contests.

RESULTS

1. Does appendotomy of Legs I reduce *T. planiceps*' fighting ablity?

Intact males won 12 of 17 contests against same-sized rivals that were missing one Leg I (test of independence, $X^2 = 5.76$, $P < 0.05$), and intact females won 18 of 25 contests against same-sized rivals that were missing one Leg I (test of independence, $X^2 = 9.68$, $P < 0.005$).

Males that were missing one Leg I won 9 of 14 contests against same-sized rivals that were missing both Legs I (test of independence, $X^2 = 2.29$, *NS*) and females that were missing one Leg I won 13 of 21 contests against same-sized rivals that were missing both Legs I (test of independence, $X^2 = 2.38$, *NS*). Pooling data from males and females, spiders that were missing one Leg I won 22 of 35 contests against same-sized rivals that were missing both Legs I (test of independence, $X^2 = 4.63$, $P < 0.05$).

Intact males won 13 of 15 contests against same-sized rivals that were missing both Legs I (test of independence, $X^2 = 16.13$, $P < 0.001$) and intact females won 15 of 20 contests against same-sized rivals that were missing both Legs I (test of independence, $X^2 = 10.00$, $P < 0.005$).

2. Do absence of Legs I and size interact as determinants of fighting ability?

Both more-injured and less-injured spiders were more likely to win when larger than their rivals (Figs 1 & 2). That is, size remains an important measure of fighting ability for all three classes of injury asymmetry for both males and females. The broadly-overlapping and discontinuous distribution of points makes it difficult to assess the actual degree of disadvantage caused by appendotomy of Legs I in terms of an equivalent to size difference. However, the scatter of points suggests that the cost of appendotomizing a Leg I on fighting ability is equivalent to c. 5 % of cephalothorax width for females, and 5-10 % of cephalothorax width

for males.

Although relative size and injury are important predictors of contest outcome, other variables also appear to be important, as the points are very scattered with respect to both size and injury state. This was especially evident for contests between females.

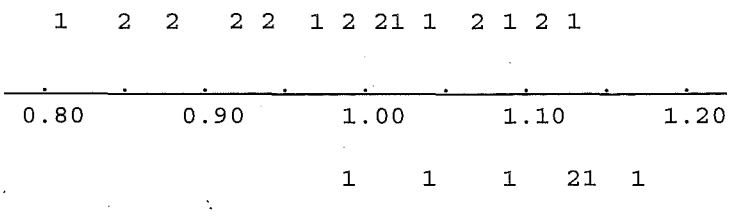
3. Do *T. planiceps* compensate behaviourally for absence of Legs I?

Neither male nor female *T. planiceps* used other legs for visual displays when Legs I were missing. Males that were missing one or both Legs I approached the other spider in the usual fashion, with palps arched and leaning sideways after each bout of oblique walking. Spiders that were missing one Leg I postured and waved with the remaining Leg I, but never postured or waved with Leg II on the other side (Fig. 3).

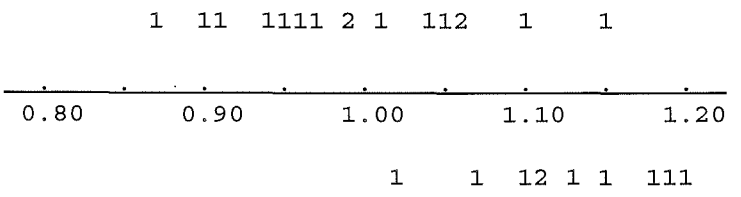
When injured spiders leaped at rivals, they did not modify the use of Legs II. Spiders that were missing one Leg I flicked the remaining Leg I upward first, and then flicked both Legs II upward together as they extended legs III and IV to leap. When one spider leaped at another, there were no instances of Legs II being used to fend-off rivals (intact spiders fend off leaping rivals with type 3 off-erect Legs I; Chapter 2).

Spiders that were missing Legs I approached each other with Legs II-IV serving their usual locomotory function but once the spiders were embracing, males used Legs II for some functions usually performed by Legs I of intact males. Males usually type 2 embraced at first, with legs II-IV remaining on the substrate. These type 2 embraces were usually brief, lasting only 1-10 s. Sometimes, Legs I were next moved outwards and spiders switched to type 1 embraces. Males that were missing Legs I often raised Legs II to oppose a rival's Legs I during type 1 embraces. However, if more-injured males did not raise Legs II, less-injured rivals often left Legs I extended c. 75° out to the side and unopposed, with the tarsi resting on the substrate.

a) Intact (above line) *versus* Missing one Leg I (below line) (N = 29)



b) Missing one Leg I *versus* missing both Legs I (N = 26)



c) Intact *versus* Missing both Legs I (N = 17)

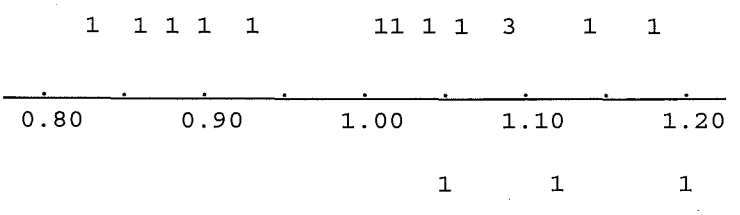
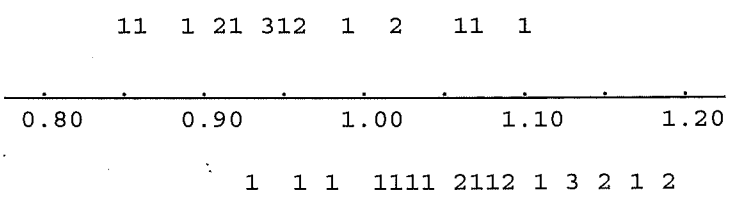
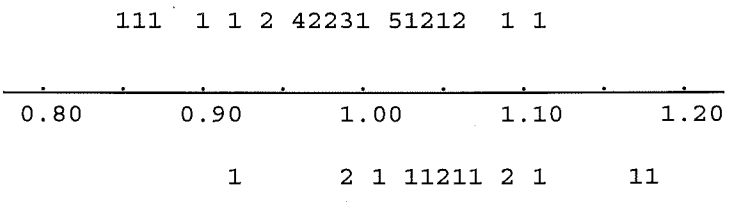


Figure 1. Outcome of contests between male spiders that differed in size and injury state. Scale is relative cephalothorax width of more-injured / less-injured spiders, numbers refer to the number of contests that were won at each relative size.

a) Intact (above line) *versus* Missing one Leg I (below line) (N = 40)



b) Missing one Leg I *versus* Missing both Legs I (N = 47)



c) Intact *versus* Missing both Legs I (N = 36)

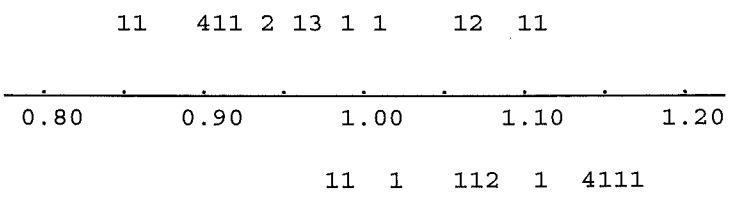


Figure 2. Outcome of contests between female spiders that differed in size and injury state. Scale is relative cephalothorax width of more-injured / less-injured spider, numbers refer to the number of contests that were won at each size.

Males that were missing Legs I never grappled with Legs II, although they occasionally hooked and pulled with Legs II (Fig. 4).

Females missing Legs I also used Legs II for some functions that would otherwise have involved Legs I. When in type 1 embraces, females missing more Legs I than rivals usually raised Legs II to oppose the Legs I of rivals. When Legs I of females that were in type 1 embraces were opposed by a rival's Legs II, less-injured females bent the tarsi of Legs I downwards. The tarsal claws of the more-injured female's Legs II contacted the less-injured rival's Legs I midway along the downward-pointing tarsi (males never did this). Otherwise, embraces between females that differed in injury state resembled embraces between intact females with the spiders pushing against each other until one spider decamped.

During contests between intact males and males that were missing both Legs I, males that were missing both Legs I moved more frequently than intact males (Fig. 5, Wilcoxon signed-ranks test, $P < 0.01$). Intact males moved more frequently during contests with rivals that were missing one, rather than both, Legs I (Fig. 5, Mann-Whitney U test, $P < 0.01$). Males that were missing one Leg I moved more frequently during contests with intact rivals, rather than rivals that were missing both Legs I (Fig. 5, Mann-Whitney U test, P 0.05-1.0).

During contests between females missing one Leg I and females missing both Legs I, females missing both Legs I moved more frequently than females missing one Leg I (Fig. 6, Wilcoxon signed-ranks test $P < 0.05$). During contests between intact females and females missing both Legs I, females missing both Legs I moved more frequently than intact females (Fig. 6, Wilcoxon signed-ranks test, $P < 0.05$).

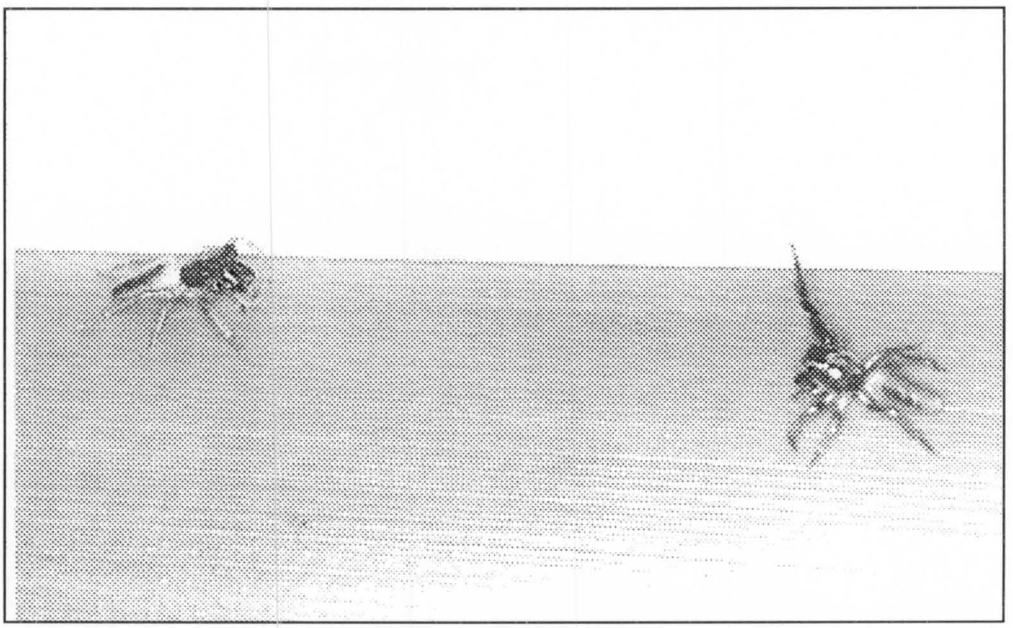


Figure 3. *Trite planiceps* male missing one Leg I postures with the remaining Leg I while approaching a rival that is missing both Legs I. Neither spider uses Legs II differently to intact spiders.

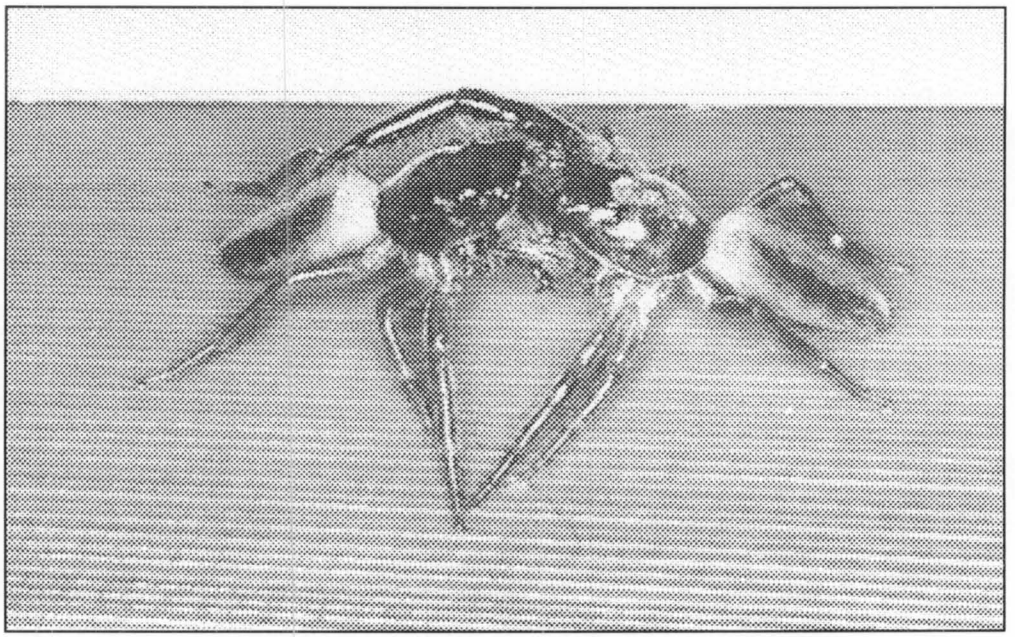


Figure 4. *Trite planiceps* male missing one Leg I embracing with a rival missing both Legs I. The spider missing one Leg I is hooking and pulling with the remaining Leg I.

4. Does appendotomy influence contest duration or maximum esalation?

Median durations of all types of contest were between 10 and 17 s. There was no evidence that interaction duration was influenced by which spider won the contest for any test type (Mann-Whitney U test, all comparisons *NS*). There was also no evidence that interaction duration varied with type of contest (e.g., intact *vs.* missing one Leg I compared with intact *vs.* missing both Legs I) for either males or females (Mann-Whitney U test, all comparisons *NS*).

Absence of Legs I also did not influence whether contests escalated to embracing (Fig. 7, test of independence, all intra-sexual comparisons *NS*) although contests between males more frequently escalated to embracing than did contests between females (test of independence: Intact *vs* Missing one Leg I, $X^2 = 4.74$, $P < 0.05$; Missing one Leg I *vs* Missing both Legs I, $X^2 = 13.26$, $P < 0.001$; Intact *vs* Missing both Legs I, $X^2 = 4.02$, $P < 0.05$).

Contests between females more frequently involved one spider leaping at the other than did contests between males (Fig. 8, test of independence: Intact *vs* Missing one Leg I, $X^2 = 6.06$, $P < 0.05$; Missing one Leg I *vs* Missing both Legs I, $X^2 = 8.50$, $P < 0.01$; Intact *vs* Missing both Legs I, $X^2 = 6.51$, $P < 0.01$). Females missing both Legs I more frequently leaped at intact rivals than *vice versa* (Fig. 9, test of independence, $X^2 = 4.86$, $P < 0.05$). Females missing both Legs I also more frequently leaped at rivals missing one leg I than *vice versa* (Fig. 9, test of independence, $X^2 = 3.01$, $P = 0.05$-0.1).

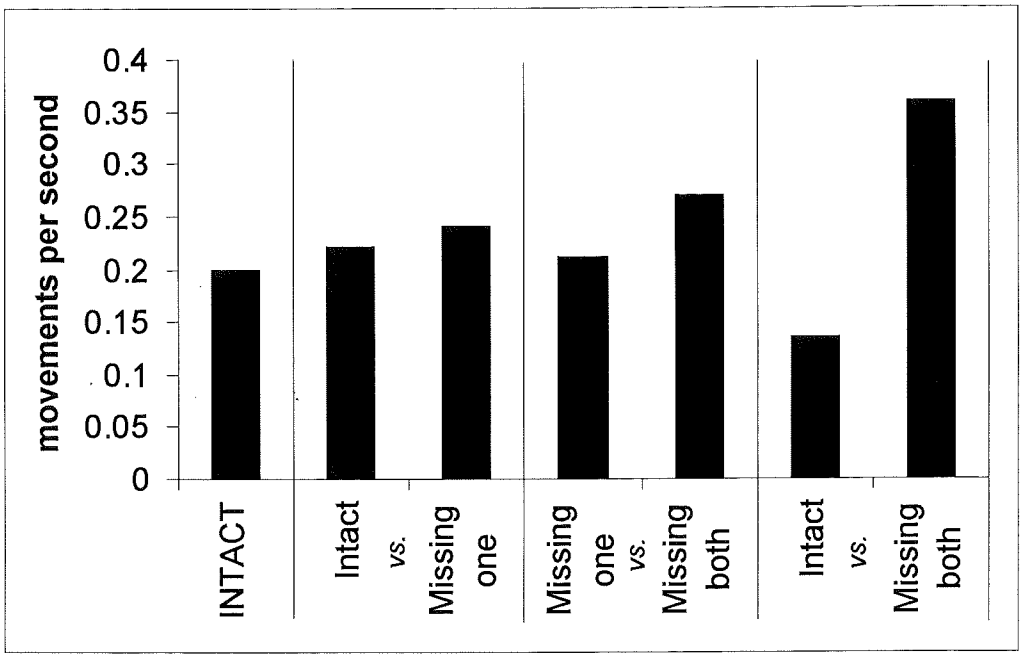


Figure 5. Effects of injury state on median frequency of locomotory movement by *Trite planiceps* males during intrasexual contests. Interactions between intact rivals from Chapter 2 are included in capitals for comparison.

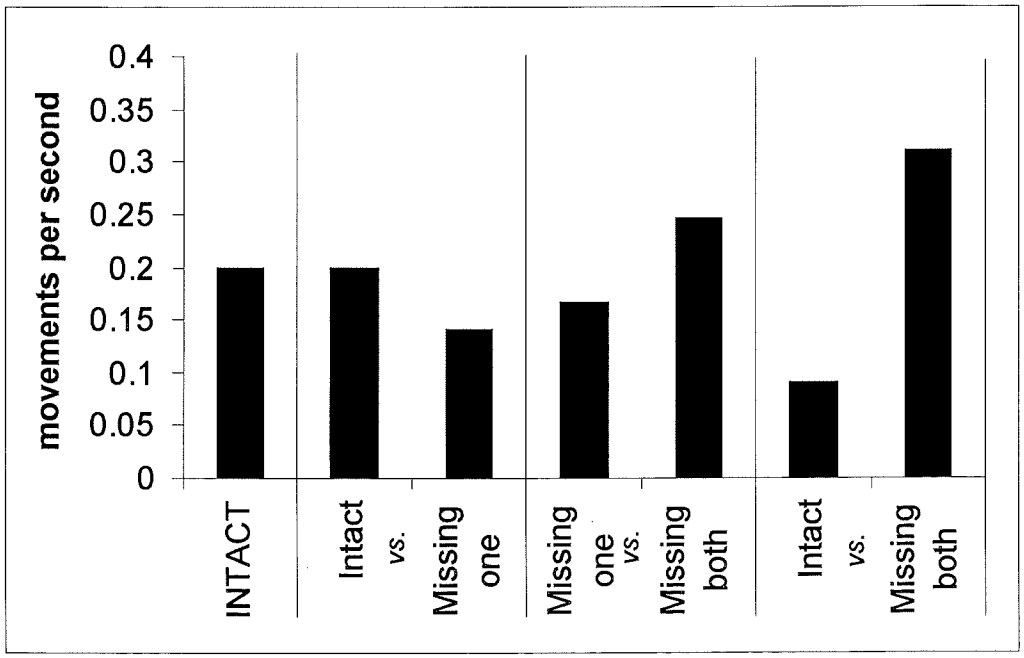


Figure 6. Effects of injury state on median frequency of locomotory movement by *Trite planiceps* females during intrasexual contests. Interactions between intact rivals from Chapter 2 are included in capitals for comparison.

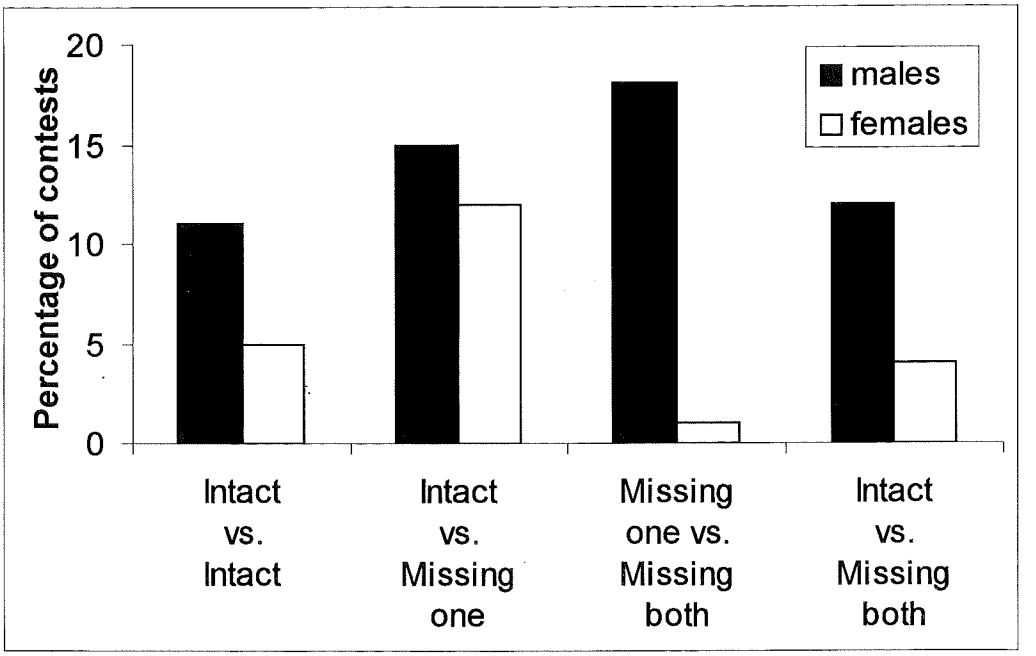


Figure 7. Percentage of contests that escalated to embracing.

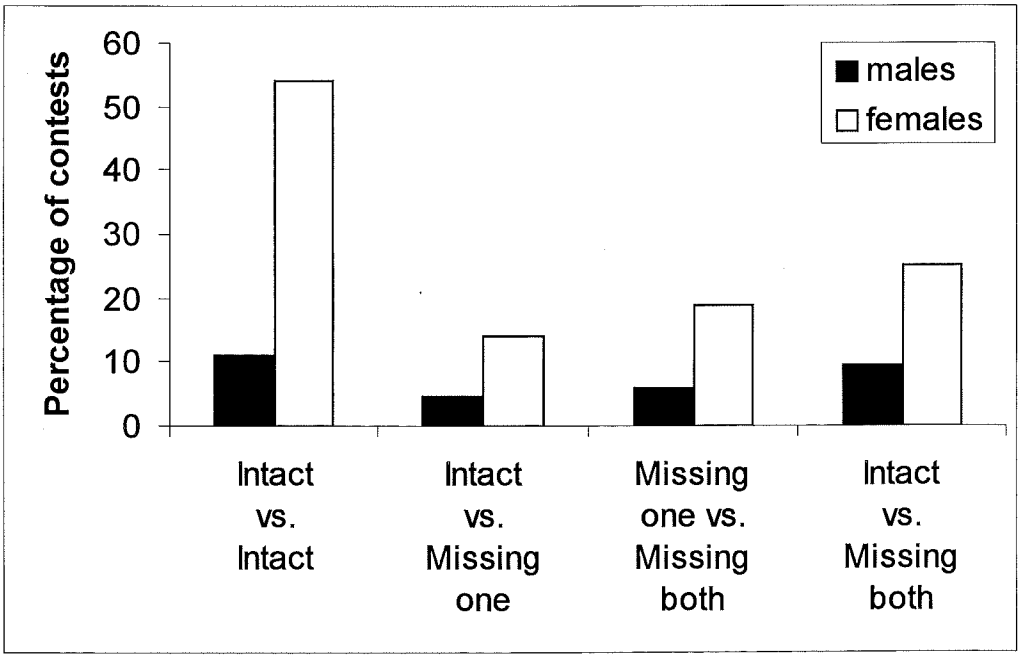


Figure 8. Percentage of contests during which one rival leaped at the other.

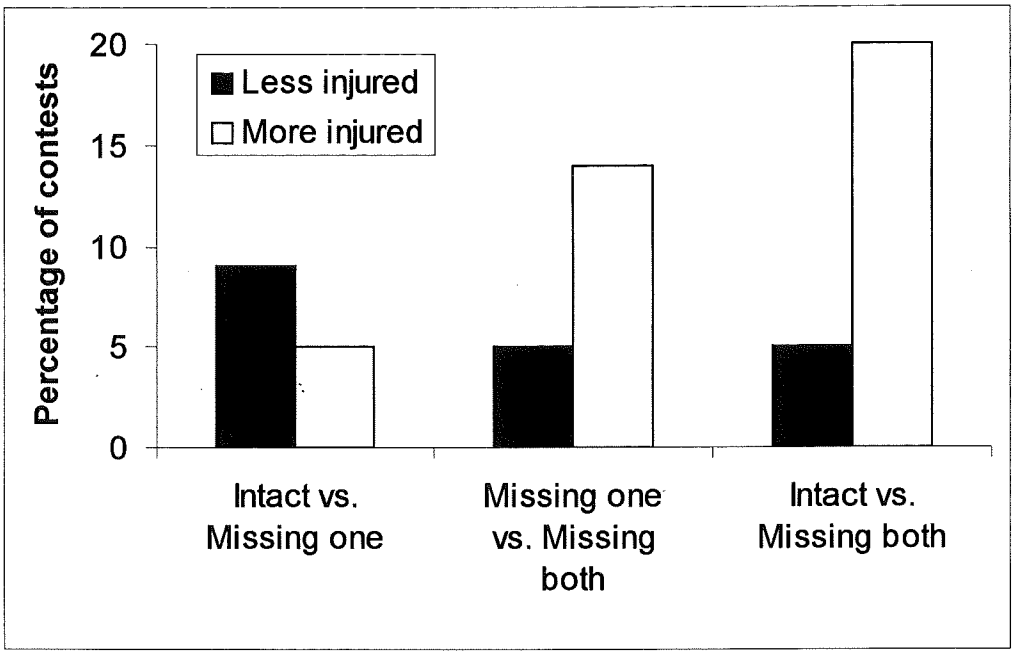


Figure 9. Percentage of *Trite planiceps* females that leaped at rivals during intrasexual contests in which rivals differed in injury state.

DISCUSSION

Do intact spiders become more bold, or do injured spiders become more timid?

Contests between salticids may be interpreted as assessment processes whereby spiders compare their own fighting ability and motivation with information that they gather about the fighting ability and motivation of rivals (Faber & Baylis 1993). Two entities must be assessed and compared: self and rival. Either or both of these information gathering processes could underlie the disadvantage experienced by injured spiders.

First, spiders might assess the injury state of rivals so that the intact spider takes account of its rival's disadvantage by escalating to a higher level than it would if the rival was intact. Second, injured spiders might assess the loss of fighting ability associated with their own injury state and respond to their own disadvantage by decreasing the level of escalation to which they are prepared to go before backing down against intact rivals. If the second process operates,

then there is some evidence that *T. planiceps* can make these assessments without experience, as the spiders used in experiments with equal-sized rivals were naive for each type of contest.

Spiders that are missing Legs I may not even assess the injury status of rivals. Instead, injured *T. planiceps* may assess their own fighting ability but assume that their rival is intact because this assumption is valid for 85-90% of encounters. Such a simple system would be encouraged if the discernibility of an opponent's injury status is low or costs of assessing injury state are high and if costs of inappropriate esalation are high.

What do *T. planiceps* assess during contests?

Relative mass of rivals is known to be a good predictor of contest outcome for some salticids (Faber and Baylis 1993), and in spiders from other families (Riechert 1978, 1984). Perhaps the tendency of *T. planiceps* that are missing Legs I to lose contests with intact rivals arises from the loss of mass associated with appendotomized legs. That is, spiders may assess their own reduced mass and compare it with the mass their rivals, possibly using some visual estimation of mass.

Alternatively, *T. planiceps* may have evolved special assessment mechanisms in response to factors that are peculiar to appendotomy, such as impaired ability to perform tasks for which intact spiders usually use Legs I. For example, spiders that are missing Legs I may have a diminished ability to injure or kill rivals (i.e., pose a decreased risk for rivals) or a reduced ability to fend-off attacks by rivals. Unlike the ability to respond to changes in mass, an ability to respond to reduced efficacy at specific functions of Legs I would require adaptation relating specifically to those functions.

Why increase motility and frequency of leaping?

That *T. planiceps* males and females that were missing both Legs I moved more frequently than less-injured rivals suggests that motion is an important aspect of intrasexual displays and that the function of displays involving Legs I may be compensated by increased motility. But what specific functions are compensated?

Increased motility may be a protean defense, as spiders that move frequently may be difficult targets for rivals to attack. However, it is difficult to explain increased frequency of leaping at rivals as a defensive behaviour. Leaping at rivals seems to entail considerably greater risk than the alternative of decamping. These behaviours may be better interpreted as 'threat displays'.

Females that are missing both Legs I may move and leap at rivals more frequently because their usual display repertoire is diminished and they substitute increased motility and leaping as the most appropriate behaviours available. That is, these behaviours may be used to replicate the same contest intensity as displays used when intact rather than as an escalation to higher contest intensity. During contests between intact *T. planiceps,* rivals often take different roles, as one spider postures and waves with Legs I while the other sits still, watching, and occasionally charging at the other spider (Chapter 2). It may be that injured spiders more frequently choose the option of high, rather than low, motility, as this option is better suited to the display repertoire available to these spiders. Some usual stages of contest escalation may be unavailable to or inappropriate for spiders that are missing Legs I. Consequently, injured spiders may escalate more quickly to behaviours that would usually be of inappropriately high intensity rather than continuing with behaviour of inappropiately low intensity.

Compensating for decreased fighting ability by performing behaviour that suggests a higher motivation to fight than their actual ability would support constitutes a bluff (Hasson

1994). The usefulness of increased motility and increased frequency of leaping at rivals as bluffs may be maintained because these behaviours may sometimes be honest displays of aggressive intent (i.e., overt attacks) and it may be difficult or costly for rivals to assess whether the leaping spider is honest or bluffing (see Adams & Caldwell 1990).

However, if increased motility and increased frequency of leaping at rivals are examples of increased bluffing that are useful in contests, it is unclear why intact spiders would not use this apparently latent ability and escalate to the level used by injured spiders. Perhaps there is some cost to bluffing that usually limits the amount of bluffing that can be used in contests. For example, it may be more costly to be revealed as a fraud at higher, rather than lower, levels of contest escalation. Perhaps the absence of Legs I alters the cost-benefit balance of bluffing so that a higher level of bluffing is favoured by injured spiders.

What is the cost of reduced fighting ability?

Why salticids fight and what is gained by winning contests is poorly understood (Jackson 1980b; Jacques & Dill 1980; Wells 1988; Faber & Baylis 1993). It is therefore impossible to make any quantitative estimate of the fitness costs brought about by decreased fighting ability following appendotomy. However, if it is adaptive to win rather than lose contests, as is almost certainly true, then immediate benfits gained through the antipredator tactic of appendotomizing Legs I are opposed by later costs of reduced fighting ability.

CHAPTER 7

Costs of an antipredator tactic: appendotomy reduces mating success in males of *Trite planiceps* (Araneae, Salticidae)

ABSTRACT

Males of *Trite planiceps* use Legs I for visual displays during courtship prior to mounting females, and for tactile displays during courtship after mounting females. In nature, however, spiders are often missing one of these legs, apparently having appendotomized them to escape predators. Absence of one or even both of these legs did not compromise male's tendency to mount or attain copulations. However males that were missing one or both Legs I more frequently copulated with only one of the female's two genital pores, made shorter individual palp applications and copulated for shorter durations overall than intact males. Consequently, injured males may transfer less sperm and be less likely to transfer sperm than intact males. Males that are missing Legs I did not use other legs to perform functions usually carried out by Legs I during either visual or tactile courtship. I discuss the trade-off between benefits of appendotomizing Legs I as an antipredator tactic and benefits of retaining Legs I for courtship and whether *T. planiceps* females discriminate adaptively against males that are missing Legs I.

INTRODUCTION

Jumping spiders (Salticidae) are well-known for their highly developed vision, sexually dimorphic colouration and ornamentation, and elaborate display behaviour (Crane 1949;

Jackson 1982a; Land 1985; Chapter 2). The origins and functions of ornamentation and courtship displays of male salticids have been debated since the pioneering studies of Peckham & Peckham (1889, 1890). The Peckhams argued in favour of sexual selection by female choice as an explanation of sexual differences in the appearance and displays of salticids (see also Jackson 1981). Other hypotheses proposed include species-recognition, sex-recognition, sexual arousal of females, habituation avoidance, cannibalism reduction (for review, see Jackson 1982a) and sensory exploitation (Clark & Uetz 1993). Nonetheless, more than 100 years after the Peckham's first studies, we still understand little about the origins and functions of sexual ornamentation and courtship behaviour in salticids.

Trite planiceps is a New Zealand salticid that, like many other salticids (Crane 1949; Richman 1982), uses Legs I extensively for visual and tactile displays during courtship (Chapter 2). After seeing females, males dance from side to side while posturing and waving Legs I in a variety of distinct displays. After mounting females, *T. planiceps* males perform tactile displays: they tap the female's abdomen with Legs I tarsi ('tap with legs') and tap the female's dorsal carapace and abdomen with their palps ('tap with palps') until the female rotates her abdomen, thereby allowing the male access to her genital pores for copulation. Males then, with Legs I, reach around the female's abdomen and loosely hold it while scraping their palps around the genital pores ('scrape with palps') until engaging the palp and copulating.

In nature, *T. planiceps* males are often missing one, and sometimes both, Legs I (Chapter 6). Absence of Legs I in this species probably results from an antipredator tactic whereby spiders discard ('appendotomize': Roth & Roth 1984) legs that are grasped or envenomated by predators (see Roth & Roth 1984; Eisner & Camazine 1983; Formanowicz 1990). *Trite planiceps* males and females that have appendotomized Legs I are disadvantaged during intrasexual contests, tending to lose contests with same-sized or slightly smaller intact

rivals (Chapter 6). In the present study, I investigate whether *T. planiceps* males that appendotomize Legs I also face adaptive trade-offs between the immediate benefits of increased survival and later costs imposed by reduced ability to perform courtship displays.

MATERIALS AND METHODS

Collection and maintenance of spiders, and removal of limbs

Trite planiceps males and subadult females were collected in the vicinity of Christchurch, New Zealand, and were maintained using standard methods (see Jackson & Hallas 1986a). Spiders were provided *ad libitum* access to house flies (*Musca domestica* L.) as prey. Subadult females were reared to maturity in the laboratory and were used in experiments within 4 weeks of maturing.

Males were randomly assigned to one of three groups: spiders that are (A) intact (B) missing one Leg I or (C) missing both Legs I. To remove a Leg I, the femur of the leg being removed was grasped with tweezers and held until the spider appendotomized the leg at the coxa-trochanter joint. For spiders in the group of spiders that were missing one Leg I, a left or right leg was randomly chosen for removal. For spiders in the group missing both Legs I, both Legs I were removed within 2h. Following removal of Legs I, all spiders were maintained for 10-14 days before being used in experiments.

Testing procedure

Only virgin females were used, and each female was used only once even if she was unreceptive. Each male was also only used in one test. Pairs comprising a virgin female and a male were selected at random from the laboratory population.

The testing arena and general procedures were the same as for tests in light in Chapter

2. A virgin female was placed on the ramp at one end of the testing arena and a male was placed on the ramp at the other end while an opaque barrier was held at the platform mid-point, preventing the spiders from seeing each other. When both spiders had walked up onto the platform, the barrier was removed so that the spiders saw each other and interacted. I recorded whether mounting and copulation occurred. I also recorded the number of palp-applications per genital pore, duration of palp applications, and total copulation durations. Whether males that were missing Legs I used other legs to perform behaviours usually carried out by Legs I of intact spiders was noted. All interactions were video-recorded and analysed later.

RESULTS

Success at attaining matings

There was no evidence that males missing one Leg I or males missing both Legs I mounted females less frequently than did intact males (Fig. 1; tests of independence, $X^2 = 0.24$ & 0.57 respectively, both *NS*). There was also no evidence that males missing both Legs I mounted females less frequently than males missing only one Leg I (Fig. 1; test of independence, $X^2 = 1.19$, *NS*). There was no evidence that males missing one Leg I or males missing both Legs I less frequently copulated with females than did intact males (Fig. 1; test of independence, $X^2 = 0.02$ & 1.81 respectively, both *NS*). There was also no evidence that males missing both Legs I copulated less frequently than males missing only one Leg I (Fig. 1; test of independence, $X^2 = 1.64$, *NS*).

Of the males that mounted females, all intact spiders, 93 % of spiders missing one Leg I, and 86 % of males missing both Legs I subsequently copulated (test of independence, all comparisons *NS*). That is, if the female allowed the male to mount he usually copulated. Additionally, there were no differences between treatments in latency from initiation of

courtship to copulation (Table I, Mann-Whitney U test, all comparisons *NS*).

Males missing one Leg I and males missing both Legs I more frequently applied their palps to only one of the female's genital pores than did intact males (Fig. 2; test of independence, $X^2 = 8.91$, $P < 0.005$ & $X^2 = 12.47$, $P < 0.001$ respectively). Total copulation durations of intact males tended to be longer than those of males missing one Leg I (Mann-Whitney U test, P 0.05-0.1) or males missing both Legs I (Mann-Whitney U test, $P < 0.001$) (Table 2). Individual palp applications of intact males tended to be longer than those of males missing one Leg I (Mann-Whitney U test, P 0.05-0.1) or males missing both Legs I (Mann-Whitney U test, $P < 0.001$) (Table 2). There were no differences between males missing one Leg I and males missing both Legs I in the frequencies with which males applied palps to one and both genital pores, duration of indvidual palp applications and total copulation duration (Fig. 2, Table 2).

Compensation for missing Legs I

Males missing Legs I did not use other legs to perform functions usually carried out by Legs I during visual 'pre-mount' courtship or tactile 'post-mount' courtship. Males missing Legs I approached females in the usual zig-zag fashion until within c. 10 mm of females and then walked forward to mount (Figs. 3 & 4: see Chapter 2). Then, after mounting, males missing Legs I performed tactile 'post-mount' courtship in a manner that could not be distinguished from that of intact males except that the usual displays involving Legs I were absent (Fig. 5; see Chapter 2).

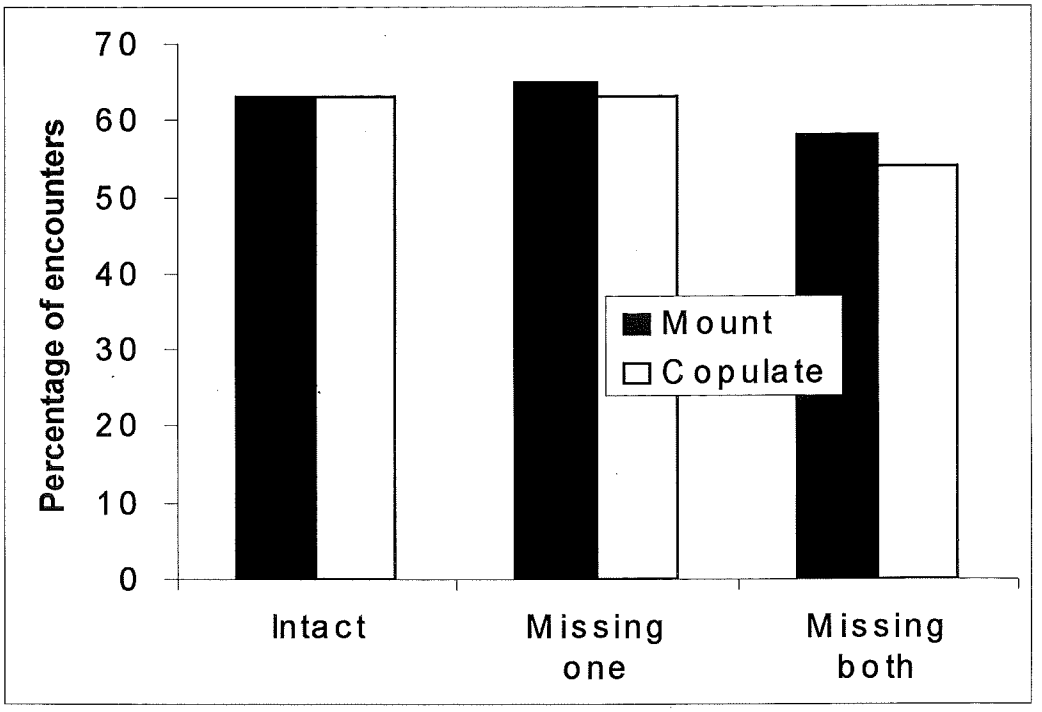


Figure 1. Percentage of *Trite planiceps* males of each injury state that mounted and copulated with females. Intact N=44; Missing one N = 23; Missing both N=28.

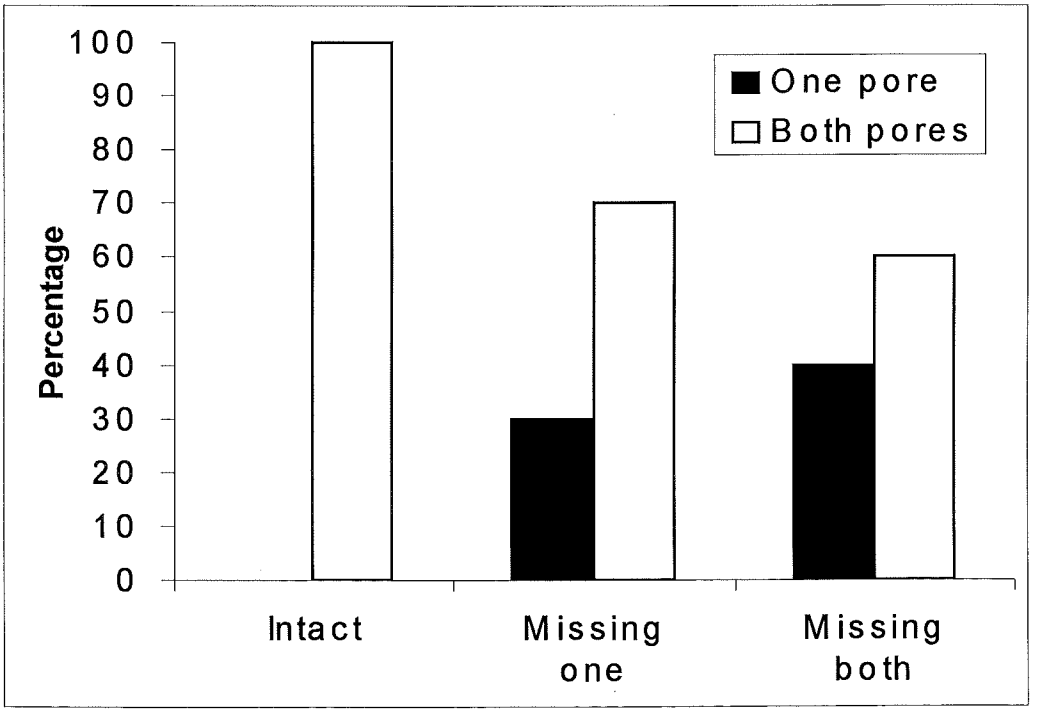


Figure 2. Percentage of *Trite planiceps* males of each injury state that applied palps to one and both genital pores during copulation.

Table 1. Latency from initiation of courtship to initiation of copulation (palp application) by *Trite planiceps* males of each injury state tested.

	Latency (seconds)		
	median	minimum	maximum
Intact	142	70	338
Missing one Leg I	159	91	901
Missing both Legs I	136	86	246

Table 2. Durations of palp applications and total durations of copulations of *Trite planiceps* males of each injury state tested.

	Duration (seconds)		
	median	minimum	maximum
a) duration of palp applications			
Intact	727	58	1449
Missing one Leg I	669	10	996
Missing both Legs I	672	78	1407
b) total copulation durations			
Intact	1447	1161	2737
Missing one Leg I	1211	534	1826
Missing both Legs I	1161	291	2383

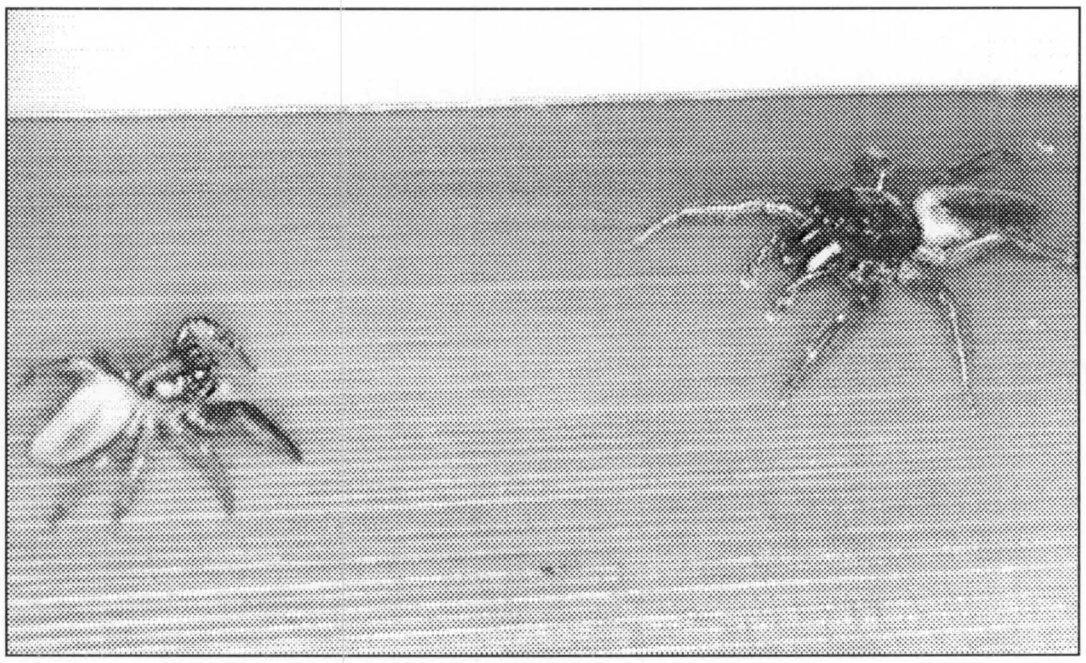


Figure 3. *Trite planiceps* male missing both Legs I courting a female (out of focus) by dancing from side to side (zig-zag dancing) without posturing or waving with Legs II.

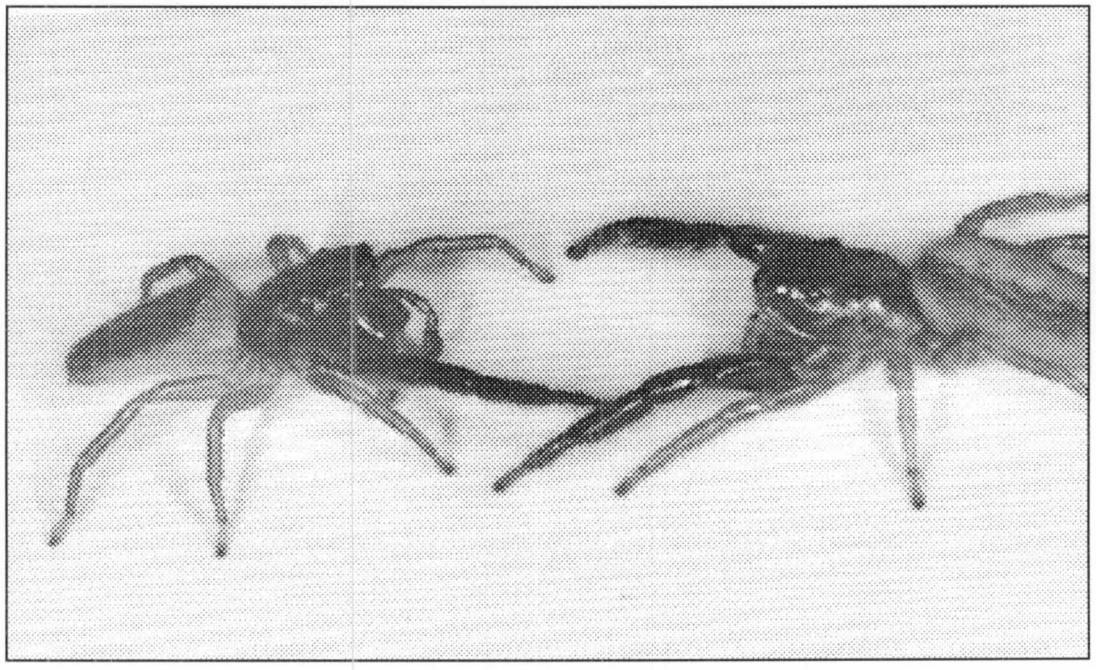


Figure 4. *Trite planiceps* male missing one Leg I advancing to mount a female. The remaining Leg I is stretched forward and raised (type 1 off-erect legs) but Leg II on the other side remains on the substrate.

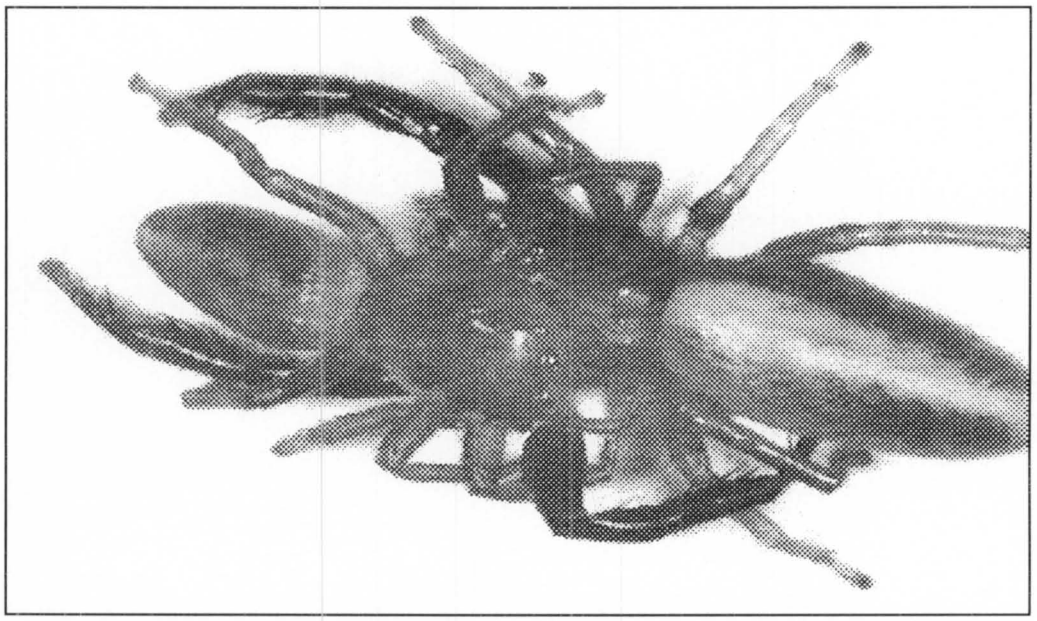


Figure 5. *Trite planiceps* male missing one Leg I performing post-mount (tactile) courtship. The remaining Leg I is used to stroke the female's abdomen, but the Leg II on the other side remains in a position similar to that of the Leg II on the side with Leg I present.

DISCUSSION

The courtship-associated costs of appendotomy

Appendotomy of Legs I by *T. planiceps* males apparently has few costs in terms of ability to attain copulations: there was no evidence in this study that males missing one or even both Legs I were less likely to copulate following courtship than were males that were intact. However, *T. planiceps* males that were missing one or both Legs I may have attained fewer fertilizations per copulation than intact males. Males that were missing one or both Legs I more frequently copulated with only one of the females' two genital pores than did intact males. It seems almost certain that less sperm is transferred if males only apply palps to one, rather than both, of the females genital pores Also, because there is no mating plug in the genital pore to which males do not apply their palps, a second male could access one of the female's genital

pores unimpeded by a mating plug. Consequently, sperm of males that copulated with, and plugged, only one of the female's genital pores may be more vulnerable to competition for fertilizations than sperm of males that copulated with, and plugged, both pores.

Individual palp applications and total copulation durations of males missing one or both Legs I tended to be shorter than for intact males. Austad (1984) suggests that, in spiders, the full complement of sperm may be transferred in a very short time, but that the point at which sperm transfer occurs is highly variable so that the longer a male copulates the better are his chances of transferring sperm. If, like *Phidippus johnsoni* (Jackson 1980a), short copulations by *T. planiceps* are more likely to result in no sperm being transferred than are long copulations, then injured males may be less likely to transfer sperm during copulation than intact males.

The behaviour of females after mating may also influence the reproductive success of males. Females of *P. johnsoni* are more receptive to re-mating after short copulations, apparently as a tactic of reproductive security (Jackson 1980a). If *T. planiceps* females are also more receptive to subsequent matings after short copulations, then sperm deposited during short copulations of injured males may be more vulnerable to competition resulting from female infidelity than is sperm deposited during longer copulations of intact males.

Do *Trite planiceps* females discriminate against injured males?

Trite planiceps females may have discriminated against injured males by (1) allowing injured males to copulate with only one genital pore and (2) limiting the time allowed to males for copulation, possibly decreasing both the maximum amount of sperm that the male can transfer and the likelihood that sperm is transferred during copulation. It may be that the female's discrimination against injured males occurs solely during post-mount (tactile) courtship. However, it is also possible that the male's pre-mount (visual) courtship influences

later decisions by the female regarding copulation. That is, we cannot rule out the possibility that the pre-mount courtship of injured males made females less likely to allow these males to copulate for long periods.

Benefits gained by females discriminating against males that are missing Legs I are not obvious, however. For example, a relationship between presence of Legs I and heritable quality of males (e.g., ability to evade predators) seems unlikely; males collected in nature missing one Leg I comprised all sizes and generally appeared healthy. 'Bad luck' in encounters with predators is probably a more important cause of appendotomy than is heritable quality. Instead, non-adaptive hypothese may be useful to explain apparent discrimination against injured males.

Discrimination against males that are missing Legs I may be a side effect of female preferences that are adaptive in other contexts. Females may discriminate against all males that have difficulty performing some aspects of courtship, possibly as a means of discriminating against males that are ill or have genital abnormalities. Because intact males are usually abundant, and mating with a malformed male of poor genetic quality may be severely deleterious for virgin females, there may be little pressure on *T. planiceps* females to discriminate between different causes of male ineptitude during courtship. Instead, females may simply discriminate against all abberant males.

Direct benefits to females appear to be the best explanation of apparent discrimination, however. *Trite planiceps* females are more frequently receptive to intact males when in shelter than when in the open (Chapter 2). This varience is most likely associated with predation risk - spiders would be relatively protected from diurnal hunters when mating inside rolled-up leaves. Females may break-off matings with males missing legs simply because they take too long, exposing them to excessive predation risk.

The functions of salticid courtship displays

It was surprising that injured *T. planiceps* males did not appear to change other aspects of their courtship to compensate for missing Legs I. Certainly, *T. planiceps* males that were missing Legs I never used Legs II to perform the visual displays that are so prominent in the courtship of intact males (see Chapter 2). Similarly, neither males nor females of *T. planiceps* use other legs to perform visual displays during intrasexual contests (Chapter 6). During intrasexual contests, both males and females of *T. planiceps* used Legs II for tactile signals usually performed by Legs I (Chapter 6). However, *T. planiceps* males did not use other legs for behaviours usually performed by Legs I during post-mount (tactile) courtship. It seems most likely that other legs are simply not suited to the tasks usually performed by the highly modified (elongated) Legs I.

Whatever the function of visual courtship displays involving posturing and waving of Legs I, it appears that these functions can usually be fulfilled reasonably completely by other components of courtship. Similarly, Crane (1949) found that elimination of secondary sexual characters in males of some salticids did not influence the acceptability of males to females as mates.

CHAPTER 8

Costs of an antipredator tactic: appendotomy reduces prey-catching ability in *Trite planiceps* (Araneae, Salticidae)

ABSTRACT

The antipredator tactic of appendotomizing Legs I is shown to conflict with the prey-catching functions of these legs in *Trite planiceps*. Although appendotomy of one or even both Legs I did not diminish *T. planiceps*' ability to catch adult house flies on the first attempt, spiders that had appendotomized both Legs I were disadvantaged during later attempts. Absence of just one Leg I did not disadvantage spiders that missed on the first attempt. During first attempts, spiders usually stalked then leaped at stationary or slow-moving house flies, whereas later attacks often involved a greatly reduced stalking phase, as spiders oriented rapidly and leaped at fast-moving house flies. Spiders that have appendotomized both Legs I appear to be disadvantaged when attempting to catch fast-moving, but not slow-moving, house flies.

INTRODUCTION

Appendotomy, the breaking-off of an appendage at a predetermined point of weakness (see Roth & Roth 1984), is a common antipredator tactic used by various arthropods (e.g., Robinson *et al.* 1970, Smith & Hines 1991a), including spiders (Eisner & Camazine 1983; Jackson & Hallas 1986a; Formanowicz 1990; Dodson & Beck 1993), echinoderms (Bowmer & Keegan 1983), annelids (Kennedy & Kryvi 1980), molluscs (Lewin 1970), and some chordates (Arnold 1984). By detaching an appendage that has been grasped or envenomated

by a dangerous opponent, the animal is able to escape, thereby avoiding more serious injury.

But the immediate advantages of this antipredator tactic may be countered by costs of diminished ability to perform other functions for which discarded appendages are used (e.g., predation, locomotion) or by nutritional and energetic costs associated with healing wounds and regenerating new appendages. Appendotomy poses such functional conflicts in lizards (Arnold 1984), crustaceans (Conover & Miller 1978; Berzins & Caldwell 1983; Smith & Hines 1991b; Smith 1992), insects (Dixon 1989; Carlberg 1992) and spiders (Hammerstein & Riechert 1988; Dodson & Beck 1993; Chapters 6 & 7). Although appendotomy of legs is very common amongst spiders (Roth & Roth 1984; Vollrath 1987, 1990), there has been little investigation of the costs and functional conflicts imposed by appendotomy in spiders.

In nature, *T. planiceps* are commonly found missing or regenerating one, and occasionally both, of their large front legs (Legs I) (Chapter 6). In all cases observed, the legs were detached at the coxa-trochanter joint, a common point of leg detachment amongst araneomorph spiders (Roth & Roth 1984). *Trite planiceps* uses Legs I to grasp, hold, and manipulate struggling prey; perhaps the advantages of appendotomizing Legs I to escape predators is offset by conflicts with the prey-catching function of these legs. If spiders that have appendotomized Legs I are less able to catch prey, then they may suffer the consequences of diminished rates of nutrition such as slowed development (Miyashita 1968; Forster 1977b), diminished fecundity (Fritz & Morse 1985; Suter 1990; Miyashita 1992; Tanaka 1992), and increased searching effort per unit of food obtained. In the present study, I investigate whether the anti-predator tactic of appendotomizing Legs I exposes *T. planiceps* to costs associated with dimished ability to catch prey.

MATERIALS AND METHODS

Intact *T. planiceps* females were collected in the vicinity of Christchurch, New Zealand, and were maintained using standard procedures (see Jackson & Hallas 1986a). The spiders were randomly assigned to one of three groups; 'intact', 'missing one Leg I', and 'missing both legs I'. Spiders were provided *ad libitum* access to house flies (*Musca domestica* L.) (hereafter referred to simply as 'flies') as prey for 4-5 days prior to removal of Legs I.

Legs were removed by inducing appendotomy. To induce appendotomy of a Leg I, the femur of the leg being removed was grasped with tweezers and force was applied so that the cuticle ruptured. The spider then promptly appendotomized the leg at the coxa-trochanter joint. For spiders in the group missing one Leg I, a left or right leg was randomly selected for removal. For spiders in the group missing both Legs I, the second leg was removed immediately after the first. All spiders were provided *ad libitum* access to flies as prey for 10-14 days following removal of limbs, and were then starved for 5 days before testing.

To begin a test, a 7-8 mm-long fly was released into an individual *T. planiceps*' maintenance cage. I recorded the number of times that the spider attempted to catch the fly, whether spiders caught the fly on their first attempt and whether spiders caught the fly within the following 10 min. I also noted the behaviours that immediately preceded capture attempts.

RESULTS AND DISCUSSION

Spiders attempted to catch the fly during the 10 min testing period in 87% of 62 tests using intact spiders, 71% of 48 tests using spiders missing one Leg I, and 83% of 48 tests using spiders missing both Legs I (test of independence, all comparisons *NS*). Also, considering only those spiders in each group that attempted to catch flies, the proportion that were succssful within the 10 min testing period was similar for the different groups (Table 1: test of

independence, all comparisons *NS*), and a similar proportion of spiders in each group that attempted to catch flies were successful on their first attempt (Table 1: test of independence, all comparisons *NS*). These results suggest that appendotomy of one or both Legs I has little or no effect on: (1) the propensity of spiders to attack flies (2) whether spiders catch flies in the 10 min period allowed and (3) the frequency with which spiders catch flies on the first attempt.

However, if they failed to catch the fly on the first capture attempt, spiders that were missing both Legs I tended to make more attempts before catching the fly than did intact spiders (Mann-Whitney U test, $P < 0.05$) or spiders that were missing one Leg I (Mann-Whitney U test, $P < 0.05$) (see Table 2). There was no evidence that spiders that were missing one Leg I were disadvantaged relative to intact spiders (Mann-Whitney U test, $P = 0.91$).

That the detrimental effects of appendotomizing Legs I were only apparent when spiders missed on the first capture attempt may be related to qualitative differences in predation sequences for the first and later attempts. In almost all instances for spiders in each of the three groups, the first capture attempt followed a sequence of stalking similar to those described by Forster (1977a). These sequences involved the spider first orienting toward the fly, then slowly stalking the fly over a distance of up to 100 mm, and concluded with the spider leaping 5-25 mm at the fly, immediately grasping it with their fangs. The fly was usually stationary or slowly walking (c. 10 mm/s) when the spider leaped. After stalking and crouching while facing a stationary fly, spiders often appeared to wait until immediately after the fly started walking before leaping.

If they failed to grasp the fly during first attack, spiders often made several attacks at flies that had not yet settled down following the first attack. These flies were walking fast (30-40 mm/s), and occasionally flying, around the cage. Attacking fast-moving flies typically involved the stationary spider rapidly orienting and then immediately crouching and leaping at

flies that ran past within c. 40 mm. If spiders failed to grasp the fly during these attacks, they sometimes immediately leaped after the fly or grabbed at the fly with Legs I, bundling it to the chelicerae.

Although loss of one or both Legs I does not greatly hinder *T. planiceps'* ability to catch flies during stalking attacks on stationary or slow-moving flies, loss of both Legs I does appear to hinder *T. planiceps'* ability to make follow-up attacks on fast-moving flies. Forster (1977b) found that *Trite auricoma* spiderlings were less successful at catching highly active rather than stationary fruit flies and *Salticus scenicus* more frequently stalk slow-moving rather than fast-moving prey (Drees 1952; Dill 1975), possibly because slow-moving prey are easier targets. It is probably more difficult for salticids to estimate location and distance of fast-moving, rather than slow-moving, prey (Forster 1979). Additionally, fast-moving prey may be more difficult to grasp. Spiders that are missing one Leg I may often be able to grasp prey by using the remaining leg, but spiders that are missing both Legs I would lack the appendages that are usually used to grasp fast-moving prey.

Table 1. Number of spiders attempting to catch the flies in the 10 min testing period (N), percent of N that caught the flies within the 10 min period, and the percent of N that caught the fly on the first attempt.

	N	% N that caught the fly in 10 min	% N that caught the fly on the first attempt
Intact	54	77.7	51.9
Missing one Leg I	34	64.7	47.1
Missing both Legs I	40	85.0	40.0

Table 2. Number of spiders that missed on the first capture attempt but caught the fly later (N) and number of capture attempts before the spider caught the fly if it missed on the first capture attempt.

	N	mean	median
Intact	16	2.88	2
Missing one Leg I	6	2.33	2
Missing both Legs I	18	4.00	3

SECTION III

Behavioural flexibility.

CHAPTER 9

Flexible oviposition timing in *Trite planiceps* Simon, a New Zealand jumping spider (Araneae, Salticidae)

ABSTRACT

In the laboratory, *Trite planiceps* (Salticidae) delayed oviposition when conditions simulating their natural oviposition sites were unavailable. Timing of oviposition in *T. planiceps* appears to be determined in part by the suitability of available sites. By discerning site suitability and delaying oviposition when suitable sites are not available, a spider in nature would gain time to find a better site. This appears to be amongst the first studies to investigate the rules underlying timing of oviposition in spiders.

INTRODUCTION

Jumping spiders (Salticidae) are selective about where they oviposit in nature, typically utilising only a narrow range of microhabitat types present in their overall habitat (see Hallas & Jackson 1986a). Some insects that are similarly choosy about where they oviposit make tactical decisions about whether to oviposit at a particular site or instead delay oviposition. These decisions are often based on the suitability of the present site and the prospects of finding a better site (Hemptinne *et al.* 1992; Rosenheim & Rosen 1991). Whether jumping spiders also have the ability to delay oviposition when preferred sites are not available does not appear to have been investigated. In the present paper, I investigate whether *Trite planiceps*, a New Zealand jumping spider that usually oviposits within the cavities formed by dry, rolled-up leaves

of New Zealand flax (*Phormium tenax*) (Forster 1979), can delay oviposition when preferred sites are unavailable.

MATERIALS AND METHODS

All tests were based on pairs of gravid, previously mated *Trite planiceps* females that were collected from New Zealand flax (*Phomium tenax*) near Christchurch, New Zealand. Gravid females were readily recognized by their distended abdomens, and that females had previously mated was evident from the presence of a distinctive mating plug. Each pair consisted of spiders of approximately matching cephalothorax width and degree of abdomen distension that were collected on the same day. Pairs always comprised spiders that were either both on or both away from nests when collected.

On the day of collection, one randomly selected member of each pair was housed in a cage (110 mm high, 110 mm diameter base, 85 mm diameter top) containing a glass tube (150 mm long, 10 mm internal diameter) inserted through the top of a cage approximately half-way between the centre and perimeter (Fig. 1). The tube was open to the cage but was blocked with a cork at the other end and was covered with an opaque black plastic sheath, thereby providing a dark, dry retreat similar to the microhabitat commonly occupied in nature (Forster 1979). Each day, the sheath was removed for 2-5 s around mid-day to check for oviposition. The other member of each pair was kept in a similar cage with a cork, instead of a tube, inserted through a 10 mm hole in the top. All spiders were fed adult house flies (*Musca domestica* L.) *ad libitum* until they oviposited. Oviposition site and latency from day of collection to oviposition was recorded for each spider.

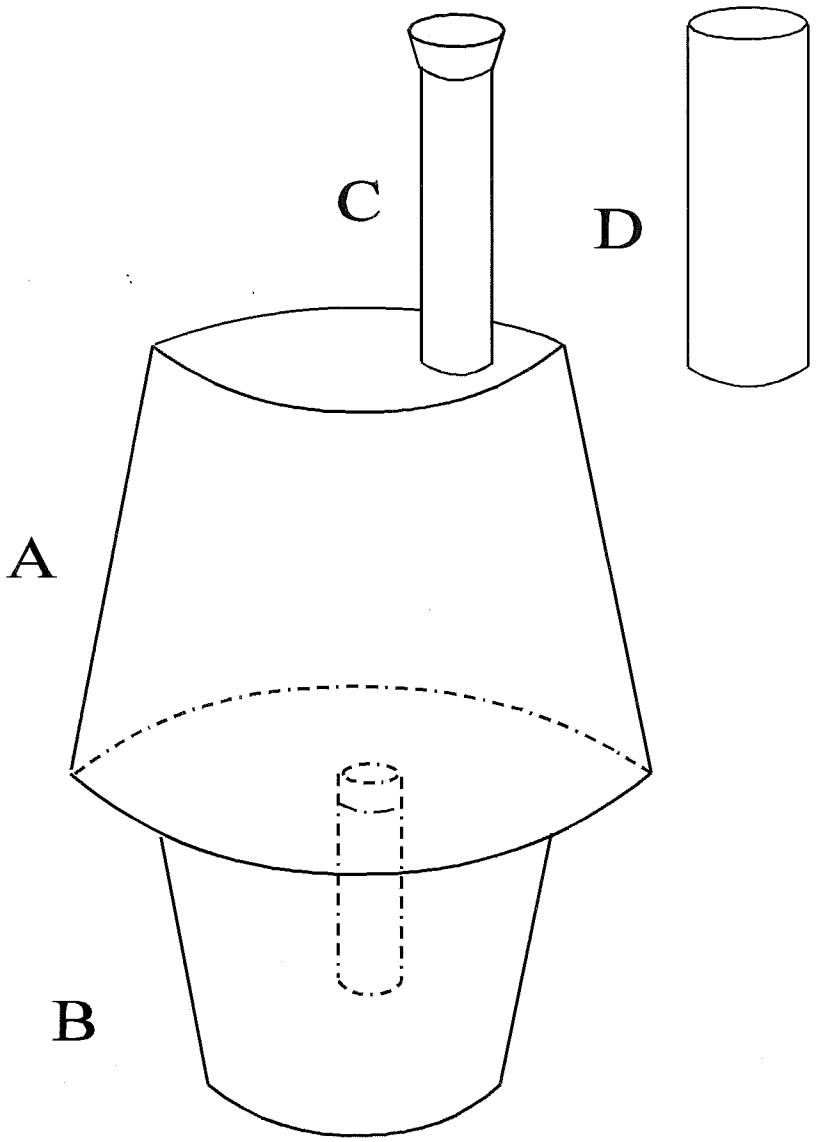


Figure 1. Cage used to investigate whether suitability of available sites influences timing of oviposition in *Trite planiceps*. A: Clear plastic cage. B: Water reservoir with cotton wick to carry moisture into the cage. C: Glass tube inserted through the roof of the cage (replaced with a cork in the treatment without access to preferred sites). D: Opaque plastic sheath placed over the glass tube to exclude light (removed in figure).

RESULTS AND DISCUSSION

All individuals in the treatment with a tube present in the cage occupied the tube as a shelter on each night and oviposited within the tube (N = 20). Apparently, the tubes were accepted as substitutes for dry, rolled-up flax leaves, the usual shelter and oviposition microhabitat in nature. When a tube was not available, spiders always oviposited at the intersection between the wall and the roof of the cage, apparently accepting this as the closest available approximation to the natural oviposition site.

All spiders in both groups oviposited, but for 19 of the 20 test pairs the female having access to a tube was the first to oviposit (McNemar test for significance of changes, $X^2 = 16.2$, $P < 0.001$). Median latency to oviposition was 3 (range 1-25) days for spiders with access to tubes and 10.5 (range 4-29) days for spiders without access to a tube (Wilcoxon signed-rank test, $P < 0.005$). These results suggest that *T. planiceps* females assess the suitability of available sites and delay oviposition when preferred sites (i.e., dry, dark tubes) are not available.

Basing decisions about whether to oviposit on the suitability of available sites would allow spiders in nature to delay oviposition when preferred sites are not available, and thereby gain additional time to locate better sites. That spiders without access to tubes eventually oviposited may reflect an inability to delay for longer, or a tactical decision to accept a poor site to avoid costs of continued delaying (e.g., time, predation risks while searching). Although there has been a great deal of research investigating the decision-making processes underlying oviposition by insects (see Rosenheim & Rosen 1991), this appears to be the first study to enquire whether a decision-making process also underlies timing of oviposition in jumping spiders. Further investigation of the decision rules governing oviposition in spiders appears to be warranted.

CHAPTER 10

Locomotory responses of *Trite planiceps* (Araneae, Salticidae) to conspecific's draglines: effects of sex, hunger, and reproductive state

ABSTRACT

Experiments were carried out to examine whether hunger or reproductive state influences the tendency of *Trite planiceps* to facilitate or avoid interactions with conspecifics by associating with or avoiding their draglines. Neither well-fed nor starved males or females showed any tendency to associate with or avoid areas containing draglines deposited by same-sex conspecifics. Males preferentially associated with areas containing draglines deposited by females both when well-fed and when starved. Although well-fed females (virgin and mated) ignored male's draglines, starved females tended to associate with areas containing male's draglines. Hunger-dependent association by females with draglines deposited by males is interpreted as part of a foraging tactic in which females only associate with male's draglines when seeking males as prey.

INTRODUCTION

Jumping spiders (Salticidae) have acute vision that sets them apart from other spiders (Blest & Price 1984; Land 1985). Not surprisingly, most research investigating the behaviour of salticids has emphasised the unusual behaviours mediated by acute vision (for review, see Richman & Jackson 1992). But female salticids are also known to communicate with males using dragline-bound pheromones. These pheromones apparently function as 'mate attractants'

(Yoshida & Suzuki 1981; Chapter 3) or as cues for species and sex identity (Jackson 1987). In this study of *Trite planiceps*, I investigate: 1) whether males produce pheromones that alter the behaviour of females, 2) whether males and females also communicate with same-sex conspecifics using pheromones and 3) whether decisions about whether to associate with or avoid draglines are influenced by hunger state or reproductive state, variables that could influence the pay-offs of interaction.

MATERIALS AND METHODS

Maintenance of spiders and testing procedures

Trite planiceps were obtained from a population living in New Zealand flax (*Phormium tenax*) near Christchurch, New Zealand. Spiders were maintained in a laboratory using standard methods (Jackson & Hallas 1986a), and were provided *ad libitum* access to house flies (*Musca domestica* L.) as prey.

The testing procedures used in the present study were the same as for tests of substrate preference in Chapter 2. Only adult spiders that possessed all appendages were used because loss of appendages is known to reduce fighting ability in *T. planiceps* (Chapter 6), and could influence pay-offs associated with response to draglines.

Experimental comparisons

To assess whether spiders were attracted to or repelled by draglines, the amount of time spent on draglined and clean half-arenas for each type of test was compared. Male and female spiders were tested both on the draglines of same-sex and opposite-sex source-spiders. Only mated females were used for tests of females spiders on the draglines of conspecific females.

To assess the effects of feeding state on preferences for draglined areas, spiders were

tested using two feeding states: 'well-fed' and 'starved'. Well-fed spiders had *ad libitum* access to prey prior to testing, whereas starved spiders were not fed for 7-9 days before testing. To assess the effects of reproductive state on response of females to draglines deposited by conspecific males, female spiders were tested in two reproductive states: 'virgin' and 'mated'. Virgin females were not later used in tests as mated females.

To determine whether a particular group (e.g., well-fed males) preferred one side of the arena over the other, the relative amount of time spent on each side of the testing arena was compared using Wilcoxon signed ranks test. To determine the effects of feeding state (well-fed *vs* starved) and reproductive state (virgin *vs* non-virgin) on amounts of time spent on the draglined and clean half-arenas, Mann-Whitney U test was carried out on a derived measurement: 'response'. Response was defined as the amount of time spent on the draglined half-arena minus the amount of time spent on the clean half-arena.

RESULTS

Responses to draglines deposited by same-sex spiders

There was no evidence that either well-fed ($P = 0.92$) or starved ($P = 0.49$) *T. planiceps* males preferred either the draglined or clean side of the arena when draglines deposited by conspecific males were present (Table 1). There was also no evidence that either well-fed ($P = 0.16$) or starved ($P = 0.82$) *T. planiceps* females preferred either the draglined or clean side of the arena when draglines deposited by conspecific females were present (Table 1). There was no evidence of any hunger-related difference in response to draglines deposited by same-sex spiders for either males ($P = 0.64$) or females ($P = 0.29$).

Responses of males to draglines deposited by mated females

Both well-fed ($P < 0.01$) and starved ($P < 0.05$) *T. planiceps* males spent more time on the draglined side than on the clean side of the arena when draglines deposited by conspecific females were present (Table 1). There was no evidence of hunger-related difference in response of males to the draglines of conspecific females (well-fed *vs.* starved, $P = 0.87$).

Effects of reproductive state on responses of females to draglines deposited by males

There was no evidence that well-fed mated females preferred the draglined or clean side of the arena ($P = 0.99$), but starved mated females spent more time on the side containing draglines deposited by males than on the clean side of the arena ($P < 0.005$) (Table 1). Also, starved mated females spent more time on the draglined side of the arena than did well-fed mated females (well-fed *vs.* starved, $P < 0.05$).

As for well-fed mated females, there was no evidence that well-fed virgin females preferred the draglined or clean side of the arena ($P = 0.29$) but, like starved mated females, starved virgin females spent more time on the side containing draglines deposited by males than on the clean side of the arena ($P < 0.01$) (Table 1). Starved virgin females spent more time on the draglined side of the arena than did well-fed virgin females (well-fed *vs.* starved, $P < 0.05$). There was no evidence that virgin and non-virgin females responded differently to draglines deposited by males either when well-fed ($P = 0.61$) or when starved ($P = 0.42$).

Table 1. Proportions of total time spent by *Trite planiceps* adults on draglined *vs.* clean sides of the arena when well-fed and when starved.

	Condition	N	Median	Quartiles
Males on male's draglines	Well-fed	36	0.50	0.36 - 0.68
	Starved	20	0.56	0.31 - 0.74
Males on female's draglines	Well-fed	23	0.79	0.54 - 0.91
	Starved	24	0.76	0.48 - 0.92
Females on female's draglines	Well-fed	40	0.59	0.41 - 0.69
	Starved	52	0.50	0.31 - 0.69
Mated females on male's draglines	Well-fed	29	0.48	0.30 - 0.77
	Starved	42	0.64	0.55 - 0.81
Virgin females on male's draglines	Well-fed	37	0.47	0.34 - 0.63
	Starved	30	0.59	0.45 - 0.73

DISCUSSION

Trite planiceps males and females apparently ignore or fail to detect draglines deposited by same-sex conspecifics, and hunger state did not influence this tendency. Although females of *Portia fimbriata* and *P. labiata* do not discriminate between clean areas and areas containing draglines of conspecific females, males of both *Portia* species avoid the draglines of conspecific males (Clark & Jackson 1995). In contrast, *Carrhotus xanthogramma* (Salticidae) males preferentially associate with areas containing draglines of conspecific males or females (Yoshida & Suzuki 1981). Clearly, there are considerable species differences in the responses of salticids to draglines deposited by same-sex conspecifics. That hunger did not influence tendency of males to associate with draglines deposited by conspecific females, and that well-fed females were not attracted to draglines deposited by males is consistent with the general impression that male salticids assume a more active role in mate-searching than females do (Jackson 1982a,b).

There are very few records of female spiders responding to draglines or chemical cues from male conspecifics (see Holzapfel 1935; Engelhardt 1964; Ross & Smith 1979; Kronestadt 1986). In *T. planiceps*, females only responded to draglines deposited by males when starved. Why would a female spider promote interaction with a conspecific male when starved, but not when well-fed? The decision of whether to ignore or associate with draglines appears to be based on foraging rather than mating considerations: hungry females may use pheromones to find males as prey. Tietjen & Rovner (1982) suggested that male-produced pheromones might inhibit sexual cannibalism in some spiders. If only starved, predatory, *T. planiceps* females are attracted to male's draglines only as a foraging tactic, then the pheromones associated with the draglines of *T. planiceps* males may sometimes have the opposite effect in this species.

CHAPTER 11

Studying the evolution of behaviour in jumping spiders: toward a more holistic perspective?

1. Introduction

Jumping spiders (Salticidae) present ethologists with remarkable potential as research subjects. Having complex eyes and acute vision, these spiders are unique amongst arachnids in the degree to which visual cues mediate their behaviour. They are diurnal predators that rely almost exclusively on vision to find and identify prey, and then to mediate hunting sequences (Forster 1977a, 1982a; Freed 1984; Edwards & Jackson 1993). Salticids also rely on vision when navigating (Hill 1979; Tarsitano & Jackson 1992; Jackson & Wilcox 1993a) and communicating with conspecifics by way of elaborate visual displays (Crane 1949; Jackson 1982a,b; Richman 1982). Salticids are gaining a high profile in ethology as their potential is being realized in a wide range of literature. Research into salticid behaviour appears to have reached a point where it may be time to survey 'the big picture', and generally consider the appropriateness of the overall research strategy.

As in studies of animal behaviour generally, most studies investigating the evolution of salticid behaviour have been based on 'the functional approach' (Jamieson 1986), also called 'the adaptationist program' (Gould & Lewontin 1979; Mayr 1983). The functional approach emphasises natural selection as a mechanism directing evolution and tends to be 'reductionist', investigating the evolution of each character more or less independently rather than explicitly considering animals as 'integrated wholes' (Gould & Lewontin 1979; Hughes & Lambert 1984;

Oyama 1988). The functional approach has been criticised for failing to consider alternatives to natural selection (e.g., Jamieson 1986; Hailman 1988) and for being excessively reductionist, paying insufficient attention to interactions between characters (Gould & Lewontin 1979; Gray 1988). However, the relevance of these criticisms to studies of salticid behaviour has rarely been considered (but see Jackson 1992). In the present review I ask whether the functional approach as it applies to studies of salticid behaviour places too much emphasis on natural selection or is excessively reductionist. These questions lead to related questions of whether greater consideration should be given to non-adaptive hypotheses and whether a greater effort should be made to interpret the evolution of salticid behaviour in a more holistic manner (see Mayr 1983; Gray 1988).

As illustration, I discuss some of the types of inter-relationships that may occur between different characters in the evolution of salticid behaviour. This review is not intended to be an exhaustive account of all selection pressures and constraints historically and currently influencing the behaviour of salticids. Instead I choose some examples that promise to be particularly instructive. That is, these are examples where a more holistic approach appears especially likely to provide insights that could be easily overlooked when a more strictly reductionist approach is adopted. By discussing the multitude of factors that might operate on the evolution of some key characteristics of salticids, we may gain insights into the complex ways in which different characteristics may interact during the evolution of behaviour.

2. Ecological and evolutionary cascades

Because characters interact in complex relationships, change in one character may lead to subsequent changes in other characters, leading to changes in still other characters and so on. A change in one characteristic may move an animal through a continuous series of

'adaptive zones' (Simpson 1953) that alter the demands and constraints over a wide array of characters until a new equilibrium suite of character states is reached. Gray (1988), in particular, developed this idea and termed these effects 'ecological and evolutionary cascades' whereby evolution may be considered 'autocatalytic'. In this section, I discuss interdependence between certain salticid characters to illustrate how common ecological and evolutionary cascades may be, and how simply they might start out.

2.1 Nesting sites and nest structure are related

Although some species are exceptional (Jackson & Hallas 1986a; Jackson 1990a,b,c), most salticids shelter and oviposit within tubular nests that completely enclose the spider and its eggs (Hallas & Jackson 1986a). The physical structure of nesting microhabitat appears to be an important influence on the design of nests in some species. For example, *Trite planiceps, Marpissa rumphi* and *Euryattus* sp. live in cavities formed by rolled-up leaves (Holm 1940; Forster & Forster 1973; Forster 1979; Chapter 2; Jackson 1985a) and are unusual in that their nests lack walls and roofs. Instead, females of each species oviposit on an unenclosed silken platform constructed against the interior wall of the rolled-up leaves (Holm 1940; Chapter 2; Jackson 1985a). It seems that some of the functions usually carried out by walls and roofs of nests in other salticid species (e.g., exclusion of free water: Jackson 1979) may be substituted by the physical structure of dry rolled-up leaves. Similarly, *Thiania* spp. oviposits in the sheltered cavity between leaves that the female binds together with silken rivets. Like *T. planiceps, M. rumphi* and *Euryattus* sp., *Thiania* spp. builds an unenclosing nest. Communicating behaviour is shaped to some extent by nest structure as salticids use the nest as a medium for vibratory communication. Hence we might say that changes in habitat lead to a cascade of changes in nest structure and then in communicating behaviour.

2.2 Relationships between habitat and mate-searching behaviour

Males of some salticids begin intensive mate-searching behaviour after encountering draglines deposited by conspecific females. For example, males of *Menemerus bivittatus, Phidippus audax, Portia labiata, Portia fimbriata,* and *T. planiceps* all preferentially associate with substrates that contain draglines recently deposited by females rather than substrates without draglines (Richman 1982; Oden 1981, in Pollard *et al.* 1987; Clark 1993, Chapter 3). Also, males of *Carrotus xanthogramma* alter their locomotory behaviour when on areas recently walked over by conspecific females and more frequently recognise prospective mates when female's draglines are present (Yoshida & Suzuki 1981). However, there has been little investigation of other cues used by male salticids to find females after they have encountered a female's draglines.

Males of some salticids may simply search for females directly (Yoshida & Suzuki 1981). But females of many salticids are rarely found away from nests and usually build nests that are hidden from view under stones or loose bark, or inside rolled-up leaves (e.g., Jackson & Harding 1982; Jackson 1985a; Jackson *et al.* 1990; Chapter 2). Males of these species might first try to find microhabitats occupied by females and then search more directly for females. There is some evidence that *T. planiceps* males, after encountering a female's draglines, do seek out sites that are likely to contain females (Chapters 2 & 3). After encountering a female's draglines on a rolled-up leaf, *T. planiceps* males move in an erratic manner, frequently stopping, palpating the leaf surface and looking around until they find an opening to the rolled-up leaf, a habitat feature that is strongly associated with presence of females. Clearly, changes in habitat preferences of females should have a follow-on effect on the mate-searching behaviour of males as different cues become associated with female distribution.

2.3 Effects of habitat on intraspecific communication

Although salticids are best known for their visual displays (Peckham & Peckham 1889, 1890; Crane 1949; Jackson 1982a; Richman 1982; Clark & Uetz 1993, 1994), most also use vibratory signals to communicate with conspecifics inside nests, a context in which visual displays would be inappropriate (Jackson 1992). That is, male salticids have two distinct display repertoires, and use the repertoire that is suited to the current site. Perhaps there are evolutionary parallels between intraspecific and interspecific variation in signalling behaviour; intraspecific variation in sites occupied leads to within-individual variation in signalling and interspecific variation in sites may lead to species differences in signalling.

The signalling behaviour of *T. planiceps* appears to be especially adapted for communicating in its unusual habitat (Chapter 2). Possibly the most remarkable aspect of *T. planiceps'* display behaviour is that simply seeing entrances to rolled-up leaves is sufficient to release displays in males, even when no female or draglines deposited by females are present (Chapters 2 & 3). Males extend Legs I to either side of the body ('on-erect legs') and repeatedly strike the rolled-up leaf by rapidly raising and lowering Legs I ('tapping on-erect legs') as they approach entrances to rolled-up leaves. The on-erect legs display is common during interactions between all sex and age classes of *T. planiceps* in light, and tapping on-erect legs is commonly observed during intrasexual contests in light. However, on-erect legs and tapping on-erect legs may not function as visual displays in this context. Instead, it seems more likely that these displays propogate vibratory signals to conspecifics within rolled-up leaves. Release of displays by a physical structure in the absence of cues from conspecifics has not been reported in any other salticid.

Trite planiceps males and females also have unusual vibratory signals that are used during interactions that occur in darkness within rolled-up leaves (Chapter 2). Males strike the

interior surface of rolled-up leaves with Legs I ('forward tapping'), which may propogate vibratory signals transmitted through the dry leaves. Females pulse their bodies up and down ('holding lunge'), and both males and females rapidly oscillate their abdomens up and down ('abdomen twitching'). Each of these behaviours may generate vibratory signals (see Maddison & Stratton 1988a,b). Other salticids use vibratory signals when at nests or during 'visual' interactions in light, but no other salticid is known to use vibratory signals in darkness away from nests. Displaying after seeing openings to rolled-up leaves and use of vibratory signals appear to be special adaptations for communicating in the particular microhabitat occupied by *T. planiceps*. That is, *T. planiceps*' signalling behaviour appears especially tailored to 'fit' this habitat; habitat and display behaviour are intimately linked. Changes in habitat may often be followed by adaptation in signalling behaviour.

The literature already contains an elegant salticid example of inter-relationships influencing signalling behaviour. Females of *Euryattus* sp., an Australian salticid, live within rolled-up leaves that they suspend from vegetation and rock ledges (Jackson 1985). Males recognise these nesting sites, walk onto rolled-up leaves, and perform behaviours that make the leaf rock back and forth ('shuddering'). Soon after males begin shuddering, females move out of the rolled-up leaf and are courted by males. Shuddering appears to be a signal especially designed for communicating with females hidden from view inside rolled-up leaves.

Portia fimbriata is a web-invading, araneophagic salticid that aggressively mimics prey in webs of short-sighted spiders, catching the host spider (dupe) when it approaches (Jackson & Hallas 1986a; Jackson 1992). *Portia fimbriata* also attacks other salticids away from webs. However, one population of *P. fimbriata* has evolved predatory behaviour that parasitizes the habitat-adapted intraspecific signalling of *Euryattus* sp. (Jackson & Wilcox 1990, 1993b). *Portia fimbriata* from one population visually recognises suspended rolled-up leaves as nesting

sites of *Euryattus* sp., walks down guylines onto the rolled-up leaves, and mimics the intersexual shuddering signals of *Euryattus* sp. males. When *Euryattus* sp. females are lured out of their rolled-up leaves, *P. fimbriata* attacks. The unusual nesting microhabitat of *Euryattus* sp. females has apparently led to special (intraspecific) signalling behaviour in *Euryattus* sp. males, which has in turn led to special (interspecific) signalling behaviour in *P. fimbriata* through exploitation of a pre-existing reciever template in *Euryattus* sp. females (see Guilford & Dawkins 1991; Proctor 1992; Clark & Uetz 1993). But the story goes even further. The selection pressure exerted by *P. fimbriata* on the affected *Euryattus* sp. population appears to have led to a co-evolutionary armsrace (see Dawkins & Krebs 1979); individuals in this population of *Euryattus* sp. recognise, and attack, *P. fimbriata* whereas *Euryattus* sp. from other populations are more easily fooled and caught (Jackson & Wilcox 1993b).

2.4 Habitat preference, sensory substrates and communication

Studies of salticid communication have traditionally emphasised the information content of displays, especially species and sex identification and genetic quality of prospective mates (e.g., Platnick 1971; Jackson 1982a; Richman 1982; Robinson 1982; Jackson & Hallas 1986a). However, it may also be instructive to consider alternative approaches that more directly acknowledge the importance of available substrates on the evolution of signalling.

The sensory substrate of recievers is an important influence on the evolution of signal design (see Guilford & Dawkins 1991; Proctor 1992; Ryan & Keddy-Hector 1992). Recent evidence suggests that adaptation of display to exploit pre-existing biases in visual, olfactory and tactile modalities of recievers should be emphasised in studies of communication by salticids (see Clark & Uetz 1993). Accordingly, it may be instructive to consider some of the sensory biases of salticids that may influence signal design.

The habitat occupied by a salticid species appears to be an important source of interspecific variation in resolution and sensitivity of the principal eyes. Principal eyes of species that live in very low levels of ambient light (e.g., in leaf litter under dense forest canopies) tend to have inferior resolution and superior sensitivity when compared to species that live in well-lit conditions (Blest 1985b). For any given size of eye, resolution and sensitivity are traded off against each other, as one ability cannot be improved without compromising the other (Blest 1985b; Land 1985). Because of phylogenetic differences in eye structure (Blest 1985a) and constraints on visual acuity, such as habitat illumination and spider size (Blest 1985b), there is considerable interspecific variation in visual acuity and sensitivity in principal eyes of salticids. For example, *Portia* has extremely acute vision with spatial resolution of 2.4 min of arc, whereas *Fluda* has comparatively poor spatial resolution of only 16.8 min of arc (Blest 1985b). Principal eyes of salticids may also differ in other parameters of performance including contrast definition and spectral sensitivity (see Yamashita 1985; Peaslee & Wilson 1989; Tiedemann 1993). Perhaps differences in the performance of primary and secondary eyes, and in the interpretation of visual stimuli, are important substrates for the evolution of species-specific and sex-specific colouration, badges, and displays used by salticids. Just as family differences in visual ability appear to be an important influence on complexity and design of visual displays in spiders (see Robinson 1982), differences in visual abilities between salticid subfamilies, genera and species may explain some species differences in signalling.

There are also interspecific differences in the performance of secondary eyes. For example, the posterior medial eyes of species in the primitive sub-family Spartaeinae are functional, but these eyes are vestigial and apparently relict in another primitive sub-family, Lyssomaninae, and in all advanced salticids (Blest 1985a). Little is known about the central processing of visual information or 'reciever psychology' (Guilford & Dawkins 1991) of

salticids, but it seems likely that there are interspecific differences that might influence signalling. For example, perhaps species that are more frequently attacked by diurnal predators are more prone to flee when startled. Rivals could take advantage of this by mimicing movements otherwise associated with attacks. Any sensory system sampling external information provides a substrate that may be vulnerable to exploitation by conspecifics (Clark & Uetz 1993), or even other species (Jackson & Wilcox 1990, 1993b). We should expect that changes in the sensory system or reciever psychology that follow habitat shifts or increased predation pressure will be, in turn, followed by changes in signalling behaviour.

2.5 Ritualisation and displays

Jackson & Hallas (1990) investigated how displays used in aggressive mimicry by *Portia* spp. in the webs of other spiders may have been derived, through ritualisation, from grooming and disturbance behaviours. These authors concluded that the grooming behaviours that are commonly performed by spiders after contacting webs may have been transformed and brought under the control of a motivation system concerned with predation, rather than hygiene. That is, it appears that displays used in aggressive mimicry evolved from a fortuitous side-effect of a behaviour that was initially adaptive in another context (grooming), indicating a historical relationship between grooming behaviour and predation success. Bristowe & Locket (1926), Bristowe (1941) and Crane (1949) have also suggested that the displays performed by salticids may commonly be derived through ritualisation of other behaviours that were initially used and evolved primarily in other contexts.

2.6 Relationship between sexual selection, habitat and predation

Sexual selection appears to have important relationships with foraging behaviour in

salticids. In *Phidippus audax*, males and females have different feeding strategies that reflect differences in their time budgets and food requirements (Givens 1978). Whereas *P. audax* females vary greatly over time in their foraging rate, males forage at a more or less uniform rate throughout adult life. Also, *P. audax* males prefer smaller prey than those most commonly taken by females. The feeding strategy of males most likely reflects a secondary effect of sexual selection that favours males investing more in mate-searching and less in foraging.

Males of many salticids possess elaborate secondary sexual characteristics (see Peckham & Peckham 1889, 1890; Crane 1949; Jackson & Whitehouse 1989). Possibly the most bizarre amongst these is the astonishing elongation of the basal segments and fangs on the chelicerae in males of the ant-mimicking genus *Myrmarachne*. These chelicerae are sometimes about 5 times the length of those in conspecific females, and make males 50-70% longer than females in total body length (Pollard 1994). The fangs of males, but not females, lack venom ducts, and so males are unable to use venom to immobilise prey. These elaborate chelicerae are probably maintained largely by sexual selection through their signalling functions during male-male contests and courtship (see Jackson 1982b, 1986f). However, these sexual benefits appear to have, at some time, incurred costs caused by reduced predatory efficacy; active prey are more likely to escape from males than females (Jackson 1986b). Males of *Myrmarachne* have adapted behaviourally for the encumbrance of elongated chelicerae. Rather than relying on venom, males of *Myrmarachne* leap onto prey, physically restrain their prey by lying on them, and eventually impale the prey with their fangs (Pollard 1994). Because elongated chelicerae do not appear to be a hindrance when eating eggs of other spiders, a common predatory tactic in *Myrmarachne* males and females, Jackson & Willey (1994) suggested that males may also compensate for their awkward chelicerae by making greater use of eggs as a source of nutrition than females do. Sexual selection and predatory tactics are clearly linked in *Myrmarachne*.

Trite planiceps also has unusual hunting behaviour, but in this species the peculiarity has apparently arisen from natural, rather than sexual, selection. This species is exposed to frequent encounters with dangerous intruders in darkness within the rolled-up leaves where it lives (Jackson & Harding 1982; Pollard 1984; Jarman & Jackson 1986; Chapter 5). Forster (1982b) found that *T. planiceps* can catch prey in total darkness and suggested that this species may have evolved special predatory abilities in response to the unusual frequency of encounters with intruders in dark conditions. Forsters' (1982b) prediction is corroborated in Chapter 4, a comparative study of non-visual prey-catching ability in salticids. Although many salticids caught intruders in darkness when tested in an arena where avoidance of intruders was difficult, *T. planiceps* was unusually efficient at catching intruders in darkness when tested in a spacious arena where spiders could easily avoid intruders. The relatively high frequency with which *T. planiceps* caught prey in the absence of visual cues does not appear to be dependent on the evolution of any special behaviour other than that *T. planiceps* is more aggressive than other salticids when touched in the dark. Other salticids commonly turn or move away when contacted by intruders in an arena that allows easy avoidance of intruders, but *T. planiceps* and hunting spiders of other families lacking acute vision often orient toward and attack intruders in darkness.

It seems likely that an aggressive response to intruders in darkness has been promoted by the frequency with which *T. planiceps* encounter intruders in dark, confining, situations. Other salticids may more easily avoid nocturnal intruders by decamping from their nests. Attacking intruders may be an adaptive response for a cornered *T. planiceps* whereas avoiding intruders may be adaptive in species from other microhabitats (Chapter 4). Changes in habitat preference can dramatically alter relationships with enemies, and subsequent adaptation for new relationships should be predicted.

2.7 Functions and evolutionary consequences of brood-attendance

Although the importance of natural selection as a mechanism directing evolution is fully acknowledged in the functional approach, the importance of constraints on evolution is rarely addressed directly. But conservative characters do play an important role in setting the boundaries within which other, more labile, characters may evolve (Williams 1992).

Maternal brood-attendance may be one conservative character limiting the evolutionary options of salticids. Female salticids typically remain with their brood until the juveniles disperse as fully-autonomous individuals (Eberhard 1974; Richman & Jackson 1992; Chapter 5). This behaviour is phylogenetically ancient, being prevalent amongst the primitive Lyssomaninae (Eberhard 1974; Jackson & McNab 1991) and Spartaeinae (Jackson & Hallas 1986a,b; Clark & Jackson 1994a) as well as in modern forms. In Chapter 5 I identify brood defense as an important function of maternal brood attendance in *T. planiceps*. Strong selection favouring brood-attendance likely limits the evolution of other characters. For example, a change in foraging schedule that exposed the brood to increased predation would not be favoured unless benefits of extra food outweighed costs of increased predation. Animals are not adapted optimally in each isolated character (e.g., brood-defense, foraging) but are instead limited to (at best) the most harmonious suite of characters available in the population.

3. Conflicting strategies and functions

One of the most common criticisms of the functional approach is that characters tend to be investigated in isolation (see Gray 1986). For example, there is a tendency to derive separate models for diet selection, habitat selection, mate-searching and so on. However, benefits in one strategy may be countered by costs in other strategies ('functional conflicts'). Here I discuss some of the conflicts that may arise between apparently disparate strategies.

3.1 Mating, predation, and anti-predator behaviour inter-relate in salticids

Montgomery (1903, 1909) considered the relationship between mating, predation, and antipredatory strategies, concluding that the courtship of male spiders reflects a conflict between "fear of, and desire for, the female." That is, Montgomery (1903, 1909) recognised that mating strategies, predatory strategies and antipredatory strategies overlap adaptively, each having an important influence on the other when determining the behaviour used by male spiders courting females. A male must court to mate, but must also be cautious of attacks by predatory females. Excessive caution might diminish the chances of mating and so males of many salticids likely face a trade-off between chances of mating with the present female and chances of surviving to mate with other females.

There is some evidence supporting the idea that male courtship behaviour adapts in response to likelihood of attack by females. Females of *Portia fimbriata* rarely attack males whereas females of congeneric *P. labiata* and *P.shultzi* often attack, and sometimes kill, courting males. Compared with males of *P. fimbriata*, males of *P. labiata* and *P. shultzi* are extremely cautious when courting and, unlike *P. fimbriata*, sometimes 'frantically decamp' when females move (Jackson & Hallas 1986). Males of *P. labiata* and *P. shultzi* also wait until the female is in a position that may handicap her ability to attack them before mounting, but *P. fimbriata* males appear far less cautious about mounting. Apparently, males of *P. labiata* and *P. shultzi* have evolved or maintained a more cautious courtship to improve their chances of finding later mates at the likely cost of reduced chance of success with the present female.

3.2 The costs of appendotomy

Salticids are able to discard (appendotomize) legs that are grasped or envenomated by predators (see Eisner & Camazine 1983; Roth & Roth 1984; Formanowicz 1990). By

discarding limbs, spiders diminish the risk of more serious injury but these benefits may be countered by diminished ability to perform other functions usually carried out by these legs.

Trite planiceps males and females use Legs I for signalling during intrasexual contests and suffer from reduced fighting ability if they are missing Legs I (Chapter 6). Although the reasons why salticids fight are not known (Jackson 1982*a*; Jacques & Dill 1980), it seems certain that there is greater benefit to winning, rather than losing, contests. Compared to intact individuals, *T. planiceps* that have appendotomized Legs I would less frequently recieve benefits of winning contests.

Trite planiceps also use Legs I extensively for visual and tactile signalling during courtship, and may suffer from reduced mating success if they are missing one or both Legs I (Chapter 7). Although males that are missing one or even both Legs I are accepted as mates by females following visual courtship, males that are missing one or both Legs I often only copulate with one of the females two genital pores and copulate for shorter durations overall than intact males. Consequently, males that have appendotomized Legs I may be less likely to transfer sperm, may transfer smaller quantities of sperm, and may be more vulnerable to sperm competition than intact males (see Jackson 1980; Austad 1984).

The benefits of appendotomizing Legs I to avoid predators may also be countered by costs of reduced prey-catching ability (Chapter 8). Although spiders that are missing one or both Legs I do not appear to be impaired when attempting to catch stationary or slow-moving prey, spiders that are missing both Legs I have difficulty catching fast-moving prey. If a *T. planiceps*' Leg I is grasped by a predator, then the individual spider faces a trade-off between benefits of increased likelihood of escaping alive and costs of reduced ability during contests, courtship and prey capture if it appendotomizes the leg to escape. This trade-off represents a conflict between strategies.

4. The importance of behavioural flexibility

A species with behavioural flexibility has a set of disparate behaviours and a set of decision rules specifying the circumstances under which each option is chosen (see Dominey 1984; Jackson 1992). Salticids are well-known for behavioural flexibility, especially their use of conditional strategies in communication. Males of many salticids have two courtship tactics at their disposal (courtship versatility) with the tactic chosen depending on the maturity and location of the female (Jackson 1986c, 1992; Chapter 2). When a male encounters a female in the open, he uses visual displays (type 1 courtship) but when a male encounters a female in a nest he uses vibratory displays (Type 2 courtship). Some salticids also have conditional predatory strategies (predatory versatility) whereby different predatory tactics are used against different types of prey (see Jackson 1992; Edwards & Jackson 1993).

The decision rules underlying choice of behaviour are tailored to the relative benefits and costs of each option available; the behaviour selected is the one that provides the best benefit-cost balance (i.e., is most appropriate) in the current context. There are two primary reasons why behavioural flexibility is relevant to the present review. First, demonstration of remarkable degrees of adaptive fine-tuning between behaviour of salticids and the limits within which they live provide some vindication for continued use of hypotheses founded on natural selection (see Jackson 1992). Second, the ability to modify behaviour adaptively in response to environment has been implicated both as a mechanism promoting morphological stasis and as a mechanism directing diversification in evolution (Bateson 1988; West-Eberhard 1989; Peters 1991). Condition-dependent behaviours may be 'hidden' from selection, thereby avoiding trade-offs that would be faced if these tactics were exposed to selection in inappropriate contexts. In effect, harmful inter-dependence of behavioural characters may be minimised by condition-dependent expression.

4.1 Flexibility in timing of life-history events

In nature, most salticids oviposit only in a very limited range of sites. For example, *Pellenes nigrociliatus* oviposits in suspended snail shells (Mikulska 1961), and *Thiania* spp. oviposit between leaves of certain size, shape and texture that females bind together with silken rivets (Jackson 1986a). *Trite planiceps* usually oviposits inside cavities within rolled-up leaves (Chapter 2). Salticids that require very specific microhabitats may be vulnerable to the problem of being ready to oviposit but in a situation where the usual oviposition sites are unavailable. *Trite planiceps* appears to have found a way around the problem of limiting availability of oviposition sites; females are able to delay oviposition if conditions simulating their usual oviposition sites are not available (Chapter 9). That is, gravid *T. planiceps* females have behavioural flexibility with two alternative options available: oviposit and delay. There are advantages and disadvantages to each option, and the option selected may be the one that provides the better net benefit in the present site. Ovipositing in sites other than the usual site may expose the eggs and the female to increased risk of predation, whereas delaying oviposition to find a better site may expose females to risk of predation while searching or force the female to rear her brood during an unfavourable season.

4.2 Flexibility in food preferences

Salticids in nature may sometimes be limited by access to suitable prey. As they become increasingly hungry, salticids may become more likely to hunt (Gardner 1964, 1966) and more likely to accept non-preferred prey (Drees 1952). Spider eggs are potentially a rich source of nutrition (Anderson 1978), and some salticids eat the eggs of other species (Jackson & Blest 1982b; Jackson 1986d; Jackson & Hallas 1986a,b; Jackson & Willey 1994) or even conspecifics (Jackson & Blest 1982*b*; Jackson 1988a). An individual female salticid that is

attending her brood has the options of (1) guarding the eggs from predators, thereby cashing in on the reproductive value of her eggs or (2) eating the eggs herself, thereby cashing-in on the nutritional value of eggs. The value of conspecifics' eggs to females as nutritional resources may vary with reproductive state and hunger state.

When alternative sources of nutrition are available, *T. planiceps* females eat eggs only when not attending eggs themselves; well-fed females that are attending their own eggs adopt, rather than eat, conspecifics' eggs (Chapter 5). However, if alternative nutrition is not available, *T. planiceps* females that are attending their own eggs sometimes eat their own eggs or adopted eggs of conspecifics. That is, *T. planiceps* females appear to make economic foraging decisions about whether to guard or eat their eggs, balancing the costs and benefits of treating eggs as reproductive resources and as nutritional resources.

Similar decisions may be made in the context of sexual cannibalism. Although sexual cannibalism seems rare in most salticids (Jackson 1985b; Jackson & McNab 1989b), it is commonplace in a few species (Jackson & Hallas 1986a; Jackson *et al.* 1990). Newman & Elgar (1991) suggest that sexual cannibalism should be sensitive to variables that influence the value of males as a foraging resource (e.g., hunger). This appears to be the case for *T. planiceps*. Virgin and mated *T. planiceps* females appear to ignore draglines of conspecific males when well-fed, but preferentially associate with areas containing male's draglines after being denied access to prey for 7-9 days. That is, decisions of *T. planiceps* females appear to vary in a manner that reflects the value of males as meals, not mates. *Trite planiceps* females appear to balance the costs of searching for males (e.g., costs of attacking a large and potentially dangerous quarry) against the value of finding males (e.g., nutrition), and only search for males when the benefits of finding males outweigh the costs of searching.

5. Is the functional approach appropriate for salticid ethology?

Jackson (1992) argues that the current emphasis on adaptive hypotheses in the study of salticid behaviour is appropriate, citing examples of interpopulation variation in behaviour and conditional strategies (a type of behavioural flexibility) as evidence of adaptive 'fine tuning'. That is, Jackson provides evidence of a close adaptive relationship between salticids and their environments: "the strengths of the adaptive hypotheses...are their abilities to explain matches between particular behaviours and specified factors in the salticids environment. Alternative hypotheses will win out only if they can account more convincingly for these matches."

There is a widely-held belief that behaviour may adapt more rapidly than morphology or physiology, and that behaviour may tend to lead, rather than follow, evolution in morphology and physiology (Mayr 1963; Krebs & Davies 1981; Bateson 1988; West-Eberhard 1989; Riechert 1993). Accordingly, adaptive hypotheses appear appropriate for the study of animal behavior generally, and of salticids specifically. Nonetheless, examples reviewed here also warn that non-adaptive hypotheses must not be dismissed offhand but should instead be considered complementary to, rather than opposing, adaptive hypotheses.

And what of reductionism? Reduction appears essential for the formulation of tractable hypotheses (Mayr 1983); it is impossible to study all inter-relating characteristics at once. Reduction is not necessarily a failing but is instead an important tool used by ethologists to identify relationships between characters. The real risk is that ethologists may sometimes fail to recognise the trade-offs they are making in the process of reduction. This risk may be increasing as ethologists restrict their individual research programs toward ever smaller sets of characters. Reduction is a necessary evil, but to understand salticids as animals, rather than as models for specific research issues, then we must at some stage put the pieces back together. Research must always be reductionist, but evolution is, by nature, always holistic.

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